Effects of forest fragmentation

on plant-bird mutualisms in New Zealand lowland forests

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ABSTRACT

In New Zealand, there is concern about whether native bird densities have declined so much that pollination and seed-dispersal services to plants are failing, especially in small forest remnants. I aimed to test whether there is a threshold area and isolation level under which a lack of interactions with birds adversely affected breeding systems of native plants. Through geospatial analyses I calculated effective patch areas and connectivity indices of 18 forest fragments on Banks Peninsula, Canterbury, ranging from 2.8 ha to 93.4 ha. There I measured bird densities using 5 minute counts and found that habitat connectivity (measured with the Harary index dH) rather than area affected bird densities and presence of native birds.

The bird-pollinated, bird-dispersed, gynodioecious native tree *Fuchsia excorticata* is prone to inbreeding depression, pollen limitation and seed limitation. Using the National Pollination Survey visual scoring method to measure pollen deposition on *Fuchsia* flowers, I found that female trees in 4 of 13 sites were suffering pollen limitation. Although self-compatible hermaphrodites at those sites showed no pollen limitation (as predicted from earlier work), they were likely experiencing higher local selfing rates. Fruit removal was measured as an indicator of dispersal service in 10 sites, and removal rates increased with site connectivity and with densities of silvereyes (*Zosterops lateralis*). Fruits from female trees produced higher quantities of filled seeds (linked to > 80% germination) at sites with higher connectivity. Germination trials were set up to detect inbreeding depression using fruits from 11 sites, and the difference in growth performance between offspring of obligately cross-pollinated females and self-compatible hermaphrodites reduced with increasing connectivity, suggesting higher self-pollination rates (and thus higher inbreeding depression) for hermaphrodites in isolated fragments.

Increasing patch area only improved pollination service in sites smaller than 15 ha, and had otherwise minor and mostly negative effects on plant-bird mutualisms. Patch connectivity dH was the most important fragmentation parameter, positively affecting mutualist bird populations, dispersal service, and limiting inbreeding depression. Therefore, on Banks Peninsula even small reserves (< 5 ha) can have successful plant-bird mutualisms if they maintain sufficient functional connectivity within the fragmented landscape.

"When one tugs at a single thing in nature, he finds it attached to the rest of the world."

John Muir

CHAPTER 1:

Introduction

Banks Peninsula: a fragmented landscape

(Photo Marine Aubert)

I. Habitat loss and biodiversity decline in New Zealand

Human colonization of New Zealand (by the end of the thirteenth century; Wilmshurst et al. 2008) has had dramatic consequences on its natural environment, including habitat destruction and fragmentation, exploitation of natural resources (e.g. timber, hunting of large birds, mining), and introduction of exotic plant and animal (especially mammal) species, of which some have become invasive. As a result of deforestation by intentional and accidental burnings, and conversion of land to pasture, agriculture and forestry, nearly three-quarters of New Zealand's original forest cover has been lost, and the current state of native forests is characterized by high fragmentation levels (Ewers et al. 2006). A large proportion of native forest remnants consists of post-disturbance, secondary forest (Walker et al. 2008; Ewers et al. 2005; Ewers et al. 2006). Lowland habitats, where 30% of New Zealand's threatened plants are located (de Lange et al. 2009), are the most impacted, reaching over 99% clearance in several districts (e.g. Banks Peninsula, Ewers et al. 2006). Lowland forest remnants are now typically small isolated patches embedded in pasture and farmed landscapes.

As a consequence of habitat loss, over-harvesting, and predation by and competition with introduced animals, a large number of endemic bird species have undergone severe decline (Holdaway 1989; Holdaway 1999; Innes et al. 2010). The unique geological history and long-time geographical isolation of New Zealand led its endemic biodiversity to evolve towards an atypical assemblage. The native terrestrial vertebrate fauna had almost no mammals (only 3 bat species), and was dominated by birds (Clout & Hay 1989; Holdaway 1989; Lee et al. 2010). In the absence of mammalian and reptilian predators, a substantial proportion of the endemic birds developed specialized traits, such as a large body size, or the loss of flight ability (Diamond 1984; Gibbs 2006). The lack of adaptation to exotic mammals has made most of the native biota especially vulnerable to competitors, predators, and herbivores (Blackburn et al. 2004).

Maori settlement was responsible for the introduction of the Polynesian rat (kiore, *Rattus exulans*) and dog (kurī, *Canis lupus familiaris*). At the time of European settlement, eleven additional mammalian predator species were brought to New Zealand where they rapidly became invasive, including rats (*Rattus rattus,* and *R. norvegicus*), mice (*Mus musculus*), hedgehogs (*Erinaceus europaeus occidentalis*), cats (*Felis catus*), stoats (*Mustela erminea*), weasels (*M. nivalis*), ferrets (*M. furo*), pigs (*Sus scrofa*) and possums (*Trichosurus vulpecula*). Blackburn et al. (2004) found a strong correlation between the probability of extinctions in native avifauna and the number of introduced mammal predators on oceanic islands.

The cumulative effects of habitat destruction, hunting, competition with and most importantly predation by introduced European mammals (Holdaway 1989; Holdaway 1999;

Innes et al. 2010), are responsible for extensive losses in the original avian community. Evolutionary biologist and ecologist Jared Diamond hence famously claimed that New Zealand was only left with "the wreckage of an avifauna" (Diamond 1984). Further decline within local avian populations may lead vulnerable bird species towards genetic bottlenecks and severe inbreeding depression, with consequent decrease in fertility and hatching failure (Briskie & Mackintosh 2003; Heber & Briskie 2010). New Zealand now holds the world's largest proportion of extinction-prone endemic birds, with over 20% of all native bird species being already extinct, and 48% forecasted to experience real or functional extinction by 2100 (Sekercioglu et al. 2004). The most vulnerable species quickly vanished, including 38% of the native forest birds (Holdaway 1989; Clout & Hay 1989; Tennyson 2010). In addition to these irreversible extinctions, several bird populations were radically reduced and now have restricted distributions, sometimes only remaining as small isolated communities in pest-free sanctuaries (Clout & Hay 1989; Davis 2008).

This is of particular concern for native plants relying on birds for reproduction, as mainland forest remnants may be lacking their original mutualist birds. North Island stitchbird (*Notiomystis cincta*), and South Island saddleback (*Philesturnus carunculatus)*, for instance, are efficient plant pollinators and seed-dispersers, but are now both extinct on the main islands; their respective populations of about 2000 individuals each have been confined on offshore islands, where introduced predators are absent (Clout & Hay 1989; Davis 2008).

II. Extinction debt and disruption of mutualisms in forest patches

High fragmentation of natural habitats has brought the majority of New Zealand below the level of expected extinction threshold (Ewers et al. 2006). For the past decades, conservation efforts have been increasingly promoted throughout the country in an attempt to prevent further biodiversity declines within New Zealand's natural environment. Ecological management strategies tend to focus on either native fauna, mainly through pest control and breeding programmes for the conservation and possibly translocation of threatened vertebrate species into managed nature reserves, or on the native flora, especially through ecological restoration and revegetation projects (Craig et al. 2000; Norton 2000; Norton 2009a; Norton 2009b; Clout 2001). However, some conservation plans may remain inefficient due to inadequate scales of focus, at the spatial level (e.g. protection of unsustainably small areas), at the temporal level (i.e. short-term conservation projects, Kearns et al. 1998; Lennartsson 2002; Mustajarvi et al. 2001; Quesada et al. 2003; Quesada et al. 2004; Herrera & Garcia 2010;

Robertson et al. 2011), and/or at the trophic level, such as single species approaches disregarding functional interactions and community composition. For instance, lacking the support of effective revegetation, cattle removal failed to increase the abundance of endangered Whitaker's skinks (*Cyclodina whitakeri*), but instead facilitated the proliferation of introduced pasture grasses and consequent irruptions of rodents that attracted introduced mammalian predators, which further reduced the Whitaker's skink population (Craig et al. 2000; Norton 2000; Clout 2001; Leathwick et al. 2003; Hoare et al. 2007; Walker et al. 2008; Norton 2009a; Norton 2009b).

Habitat destruction and isolation of forest fragments within modified, agriculturally dominated landscapes are known to result in immediate dramatic biodiversity loss, mainly among species with sensitive life-history traits, such as flightless birds, large-bodied animals, ground foragers, narrow-range species, habitat specialists, and short-lived species (Rathcke & Jules 1993; Sodhi et al. 2004; Fahrig 2003). However, impacts of fragmentation on the biodiversity of remnant forest patches may be delayed for several decades to centuries, as the decline of some populations may be very slow, without obvious detectable evidence. This phenomenon, referred to as 'extinction debt', depends on the time-lag after fragmentation until all local species extinctions actually occur (Diamond 1972, 1984; Tilman et al. 1994; Ferraz et al. 2003; Kuussaari et al. 2009). This time-lag may be particularly long for generalist, widespread, and long-lived species, because fragmentation has usually no significant impact on the longevity of the species, but rather affects their regeneration capacity. Recruitment failure or reductions in genetic diversity may remain unnoticeable, and can only be detected in the following generations (Wilcox & Murphy 1985; Tilman et al. 1994; Kareiva & Wennergren 1995; Turner et al. 1996; Blackburn et al. 2004; Sodhi et al. 2004; Vellend et al. 2006; Aguilar et al. 2008; Kuussaari et al. 2009; Robertson et al. 2011; Fahrig 2013).

An important example of such gradual and long-term effects is the disruption of mutualistic interactions between plant and animals (e.g. pollination, seed-dispersal, facilitation of germination) in fragmented systems, which could put plant and animal mutualists at particular risk (Rathcke & Jules 1994; Kearns et al. 1998; Lennartsson 2002; Wilcock & Neiland 2002; Hobbs & Yates 2003; Quesada et al. 2003, 2004; Harris & Johnson 2004; Aguilar et al. 2006, 2008; Robertson et al. 2011). Recently, an increasing number of studies are showing evidence of positive relationship between fragmentation, mutualism disruptions, and plant recruitment failures (Kearns et al. 1998; Mustajarvi et al. 2001; Lennartsson 2002; Quesada et al. 2003, 2004; Herrera & Garcia 2010; Robertson et al. 2011), however there has also been some uncommon evidence of positive effects of forest fragmentation on mutualistic interactions and plant reproduction at the edge of forest fragments (Burgess et al. 2006). The intensity of

fragmentation's adverse effects on local biodiversity varies both with the level of fragmentation (i.e. extent of habitat loss, isolation of remnant fragments, and nature of change in vegetation cover on the surrounding matrix) and the life-history traits of the mutualist species involved (Figure 1.1). Thus, the 'relaxation phenomenon' (i.e. the amount of extinction debt and speed of local losses) may appear very different between a single large patch, constrained within a hostile matrix, versus a group of structurally isolated small patches with sufficient functional connectivity (Wilcox & Murphy 1985; Andren 1994; Hanski & Ovaskainen 2002; Lennartsson 2002; Henle et al. 2004; Ewers & Didham 2006; Cramer et al. 2007; Kuussaari et al. 2009; Mortelliti et al. 2010; Uezu & Metzger 2011; Habel & Zachos 2012).

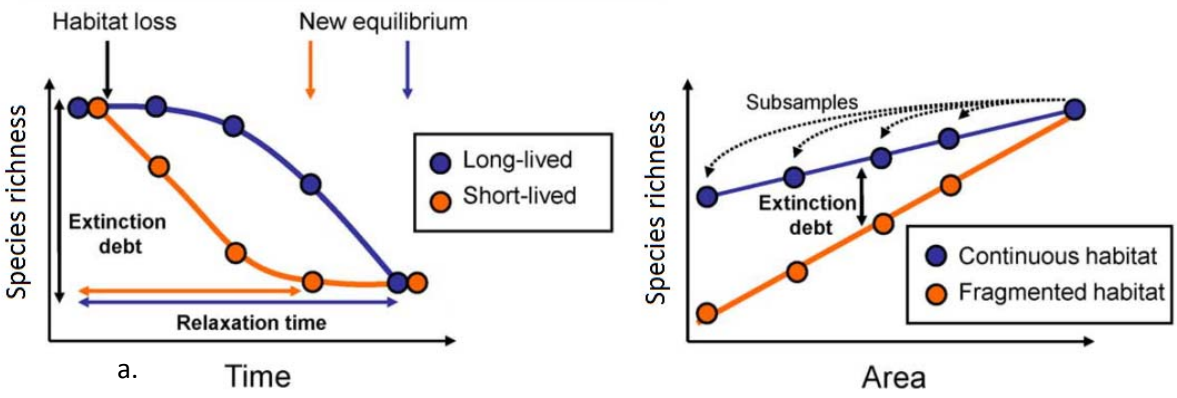

Figure 1.1: Conceptual model of extinction debt. (a) After habitat loss, short-lived species show shorter relaxation time than long-lived species. (b) Species–area relationships in continuous habitats are shallower than those in isolated patches of similar size. Immediately following disturbance, extinction debt is higher in small fragments where local extinctions tend to happen rapidly; after some time extinction debt can become higher in large patches. Both axes are on a log scale. (Kuussaari et al. 2009)

III. Plant-bird mutualisms in New Zealand

The long-time isolation of New Zealand and conjoint evolution of its native plant and animal species has led pollination and seed dispersal processes to be particularly dependent on the native avifauna (Clout & Hay 1989). Indeed, New Zealand's native flora has more reliance on birds for dispersal than is usual in the temperate zone: the high ratio of fleshy fruited species accounts for 13% of all native vascular species, and for about two thirds of the native trees (Wilton & Breitwieser 2000; Thorsen et al. 2009; Kelly et al. 2010). Moreover, a remarkably large number of native plants have been shown to rely on bird for pollination: 85 species are

regularly visited by birds, including 48 native plants which reproduction is essentially achieved by pollinator birds (Clout & Hay 1989; Kelly et al. 2010).

Nowadays, frugivory and potential seed dispersal by birds in New Zealand rely on 22 bird species, including 15 native and 7 exotic species (Kelly et al. 2006). In a review of 39 datasets from 10 different sites, Kelly et al. (2006) found that the top four seed-dispersers (accounting for 84% of fruit visitation) were native birds, including the widespread silvereye (*Zosterops lateralis*), and less commonly distributed bellbird (*Anthornis melanura*), tui (*Prosthemadera novaeseelandiae*) and kereru (*Hemiphaga novaeseelandiae*). Tui, bellbird and silvereye were also the top three pollinators of native bird-pollinated plants, accounting for 89% of flower visits (Kelly et al. 2006). Kaka (*Nestor meridionalis*), kokako (*Callaeas cinereus*), and North Island stitchbird or hihi (*Notiomystis cincta*), which have all undergone significant reduction in range and population size, are endemic species with specialized brush tongues, and would have previously been important pollinators across the mainland (Kelly et al. 2010; Anderson et al. 2011).

There is evidence globally and in New Zealand that changes in bird density have a significant influence on foraging behaviour, food preference, and competition mechanisms among bird species, including kereru, bellbird, and tui (Pyke et al. 1977; Craig et al. 1981; Stewart & Craig 1985; Clout et al. 1991; Fontaine et al. 2008; Morrison et al. 2010). Absolute reciprocal specialization in plant-animal mutualisms is very uncommon; the usual pattern consists of generalized interaction webs involving several species of both plant and animal mutualists, varying spatially and temporarily (e.g. Kearns et al. 1998; Vazquez & Aizen 2004). The low density of native bird populations in New Zealand implies a reduction in the influence of intra- and inter-specific competitive interactions, thereby favouring acute changes in diet, such as reduced visitation to food plant species with low nutritional values, or lower densities, or which expose the birds to higher predation risks (Innes et al. 2010; Anderson et al. 2011). In low-density populations of kereru, Clout et al. (1991) found that reduced competition for food resulted in higher residence times in fruiting trees and less frequent movements between forest patches.

Because of the losses in native avifauna (Diamond 1984), it is probable that some plant-bird mutualistic interactions have suffered local alterations (Holdaway 1989; Thorsen et al. 2009). Along with the significant impact of habitat destruction, high rates of pre- and post-dispersal seed predation, and herbivory, the loss of plant-bird mutualistic interactions in New Zealand constitutes a substantial threat to the regeneration ability of native bird-pollinated and fleshy-fruited species (Kelly et al. 2004, 2006, 2010; Norton 2009b; Anderson et al. 2011). Some native plants may suffer from insufficient visitation by mutualists and subsequent increase in

self-pollination (Van Etten et al. 2015): some tree species already show high levels of inbreeding depression, which has resulted in cryptic regeneration failure and population decline (Kelly et al. 2004; Aguilar et al. 2008; Robertson et al. 2011). The depletion of native birds on the mainland has proven responsible for pollination and seed dispersal failures among several native plants, including the shrub *Rhabdothamnus solandri* (Anderson et al. 2011), nikau (*Rhopalostylis sapida*; McNutt 1998), karo (*Pittosporum crassifolium*; Anderson et al. 2006), tree fuchsia (*Fuchsia excorticata*; Robertson et al. 2008, 2011), kowhai (*Sophora microphylla*; Robertson et al. 2011) and *Coprosma areolata* (Wyman 2013). These mutualism disruptions have had significant impacts on plant reproduction, and may lead to cascading effects at the ecosystem level (Anderson et al. 2011). Although dispersal seems to be generally efficient within remnant patches of native vegetation (Kelly et al. 2010), fragmentation is probably reducing the movement of seeds between patches, affecting some particular species that may be at risk locally (Wotton & Kelly 2012).

IV. Research design

Indicator plant species: Fuchsia excorticata (Onagraceae)

To investigate how habitat fragmentation affects mutualistic interactions with birds in the regeneration processes of native plants, I chose to focus on an indicator species that relies on birds for both pollination and seed dispersal. Because of its wide distribution range across New Zealand, the availability of relevant information on its mating systems, and the recent development of specific microsatellite markers, I selected *Fuchsia excorticata* (tree fuchsia, or kotukutuku) as the best candidate species. Recent studies of *F. excorticata*'s reproduction patterns have been carried out around mainland New Zealand, involving the design of reliable methods to assess site-specific pollination and dispersal services, inbreeding depression, and regeneration success (e.g. Robertson et al., 2008, 2011). These methods have proven to be accurate, reproducible, and allow for a critical comparison of results in various contexts.

Fuchsia excorticata is a long-lived New Zealand endemic tree, and the world's largest fuchsia: it can grow up to 14 m tall, with a trunk of mesomorphic wood that can reach 80 cm in diameter. Generally widespread throughout the country, it is usually found in mixed angiosperm-podocarp or *Nothofagus* forests, from sea level to c. 1000 m in elevation. Mostly present in lowland regenerating forests, where it can be locally dominant, it is typically scattered along stream banks, or persists as smaller shrubby trees along forest edges and in

disturbed habitats (Godley & Berry 1995; Dawson & Lucas 2000). One of the few deciduous native trees in New Zealand, *F. excorticata* has fire-resistant wood that is characterized by high water contents and a lack of distinctive growth rings (Godley & Berry 1995). It is a partially seral species and an important coloniser that contributes to the alleviation of land slips, stimulates secondary succession in disturbed habitats, and becomes overtopped by taller hardwood trees in late successional forests (Wardle 1964; Burrows 1995; Godley & Berry 1995; Robertson et al. 2008).

Fuchsia excorticata has a highly palatable and nutritious foliage, which makes it extremely vulnerable to brushtailed possum (*Trichosurus vulpecula*) browse: once damaged by herbivory, adult trees can die within two years of defoliation (Rose et al. 1993; Pekelharing et al. 1998; Sweetaple & Nugent 1999). In sites where heavy possum browsing has damaged the dominant fuchsia canopy, rapid tree mortality has led to the collapse of entire fuchsia populations and local extinctions (Rose et al. 1993; Pekelharing et al. 1998; Sweetapple et al. 2004). The resulting overall decline in adult *F. extorticata* densities throughout much of its range has been well documented (Rose et al. 1993; Pekelharing et al. 1998; Sweetaple & Nugent 1999; Sweetapple 2003; Sweetapple et al. 2004). In order to allow for the replacement of dying *F. excorticata* adults by newly established viable seedlings, it is essential to maintain, facilitate, or restore sustainable regeneration processes in native lowland forests (Pekelharing et al. 1998).

Fuchsia excorticata is a gynodioecious species: individual trees are either female or hermaphrodite. Its flowering season can begin as early as late winter and last until up to mid-summer, and generally varies with elevation, starting later at higher altitudes (Godley & Berry 1995). At the start of the season, flowers with a green tubular corolla develop among the leaves and directly on the trunk and branches of adult trees. At maturity, bright blue pollen is produced by the anthers of hermaphrodite flowers. When pollination occurs, this blue pollen is visually identifiable on the yellow stigma, and the corolla evolves a deep red to purple tint that lasts for 3-5 days before the flower drops off (Delph & Lively 1985). Hermaphrodite flowers are self-compatible, however selfed progeny suffer from cumulative inbreeding depression, including reduced germination, growth and survival rates (Robertson et al. 2011). Herkogamy levels (the spatial separation between the anthers and stigma) in fuchsia flowers vary between plants, potentially causing a disparity in the ability of individual hermaphrodite trees to self-pollinate (Godley 1955; Robertson et al. 2008). The co-occurrence of dichogamy and herkogamy in this self-compatible species is an indication of natural selection towards improved pollination effectiveness (Webb & Kelly 1993). Female flowers are smaller and produce less nectar than hermaphrodite flowers (Delph & Lively 1985). Pollination in female flowers is necessarily

outcrossed, and engenders offspring of both sexes in equal proportions, whereas hermaphrodites produce only hermaphrodite offspring. Consequently, sex ratios fluctuate between sites, with hermaphrodites always a majority of plants, and females generally constituting about one third (up to 40.4%, Godley & Berry 1995) of the tree fuchsia populations (Robertson et al. 2008). Both hermaphrodites and females are capable of high fruit sets, and both are susceptible to pollen-limitation (Robertson et al. 2008).

Fuchsia excorticata's fruiting season broadly lasts from late spring to early autumn; in early summer, it is usual to find trees simultaneously bearing flowers and fruits at various stages of maturity (Godley & Berry 1995). The successional period from flowering to fruiting is site-specific, starting earlier and lasting longer at warmer, dryer, lowland and coastal places than at higher elevations, where mean temperatures are lower and humidity is greater. *Fuchsia excorticata* fruits are small ovoid berries c. 12 x 5 mm. Each fruit contain 300-600 small seeds of c. 0.5 mm in diameter, equally distributed in four locules (Godley & Berry 1995; Robertson et al. 2008). The fuchsia fruit's outer skin is pale green at the immature stage, and acquires a dark purple colour as the berry ripens. The flesh of these edible berries has a sweet taste and is a preferred food of birds (Godley & Berry 1995).

Mutualist birds

The guild of mutualist birds interacting with the tree fuchsia includes its pollinators and seed dispersers. In a review of reported bird visitations to native fruits and flowers, Kelly et al. (2006) estimated the relative importance of bird species as *F. excorticata*'s pollinators and dispersers. Across 11 sites on the mainland, *F. excorticata* flowers were mainly visited by bellbirds (29.1% of flower visitation records), tui (23.1%), and silvereyes (47.2%). Stitchbird has been reported to visit *F. excorticata* flowers and is likely to have been another key fuchsia pollinator (Godley & Berry 1995). This rare native honeyeater is now functionally extinct on mainland New Zealand, it only persists on pest-free bird sanctuaries (Godley and Berry 1995, Kelly et al. 2006). Despite the considerable reduction in bellbird and tui populations within large parts of the mainland over the past 150 years (Robertson et al. 1999), bellbirds are still common in Canterbury, and a small population of tui (72 birds) has been successfully translocated for reintroduction on Banks Peninsula in 2009 and 2010 (Banks Peninsula Conservation Trust n.d.). Silvereyes are the most commonly observed of fuchsia flower visitors, but their effectiveness as fuchsia pollinators is limited, as they tend to rob the larger hermaphrodite flowers to feed on nectar, so they don't pick up pollen and are unlikely to pollinate female flowers even though they approach these from the front (Delph & Lively 1985;

Kelly et al. 2006; Robertson et al. 2008). Exotic bumblebees (*Bombus* spp.) are frequently seen on *Fuchsia excorticata* flowers, but they have also been reported as nectar-robbers (Delph & Lively 1985). This behaviour may prevent effective pollination, since damaged flowers may be mechanically impaired or discourage legitimate pollinators (Irwin & Brody 1999; Anderson 2003).

Fuchsia excorticata berries are reportedly eaten by native kereru, bellbirds, tui, silvereyes, and by exotic blackbirds (*Turdus merula*), with occasional reports of consumption by native fantails (*Rhipidura fuliginosa*) (O'Donnell & Dilks 1994; Kelly et al. 2006). The relative importance of each bird species on fruit consumption varies with local alternative food sources and bird populations (Craig et al. 1981; Burrows 1994; O'Donnell & Dilks 1994; Kelly et al. 2006). However, the efficiency of each fruit visitor as a disperser is currently poorly known (Kelly et al. 2006). Wyman et al. (2011) found that the tree weta (*Hemideina*) was opportunistically feeding on *F. excorticata* berries, but acting mostly as seed predators, and providing low quality dispersal to the small proportion of seeds remaining intact after consumption. The small and abundant *F. excorticata* seeds are unlikely to benefit from these incidental events of seed ingestion and excretion by the tree weta, nor to be affected by such subsidiary seed predation. Nevertheless, some fruit visitors may eat the berries without dispersing the seeds away from the parent, or may distribute them to unsuitable microsites, where environmental conditions are inappropriate for establishment and survival (Grubb 1977; Schupp 1995). The odds of inadequate dispersal increase with habitat fragmentation, as forest patches decrease in size and become isolated within large areas of non-colonisable matrix (Bacles et al. 2004).

Study area: Banks Peninsula

Botanist and inspirational conservationist Hugh Wilson, manager of Hinewai reserve, and author of several field guides and botanical reports, has carried out thorough botanical surveys of Banks Peninsula for numerous years, initially for the Protected Natural Areas Programme (Wilson 1992). The following description of Banks Peninsula is largely based on the information included in his most recent book, *Plant Life on Banks Peninsula* (Wilson 2013).

Banks Peninsula is an oviform headland of hilly coastal embayments, protruding into the Pacific Ocean from the eastern side of the South Island's Canterbury Plains. With a total area of about 100,000 ha, approximately 50 km long by 30 km wide, Banks Peninsula reaches its highest point at 920 m on the top of Mount Herbert, with numerous additional summits

exceeding 500 m in elevation. Geologically it is the result of accumulated outpourings from the volcanic activity of Lyttleton Volcano over 11 million years ago, Mount Herbert Volcano between 9.5 and 8 million years ago, and Akaroa Volcano about 9 million years ago, followed by intensive erosion caused by highly fluctuating climates during interglacial periods. Native vegetation was already flourishing on the flanks of the active volcanoes, probably distributed along an altitudinal gradient from subalpine forest to alpine tussockland, only periodically burnt or buried by lava flows and ash. After the last glaciation, which ended about 12,000 years ago, Banks Peninsula was entirely covered with native forest, occasionally subject to local disturbances such as fire, slips, floods, droughts, and breakages from strong winds or snowfall. Native birdlife was particularly diverse, including a little over 100 bird species present on the Peninsula.

Human settlement on Banks Peninsula occurred when the first Polynesian arrived in the 13th century A.D. Maori people impacted the natural environment by introducing dogs and rats, and by burning, altering or exploiting the land. By the end of the 18th century, about one third of Banks Peninsula's forest cover had been cleared by repeated deliberate and accidental fires (Figure 1.2a). The bare lands were used to cultivate bracken, and supplied practicable travel paths. Although no plant species are known to have been brought to extinction during Maori times, about 20 bird species vanished as a result of over-harvesting, habitat loss, and predation by kiore (Pacific rat, *rattus exulans*), including moa (Dinornithiformes), kiwi (*Apteryx* spp.), kakapo (*Strigops habroptilus*), takahe (*Porphyrio hochstetteri*), adzebill (*Aptornis defossor*), bush wrens (*Xenicus longipes*), several birds of prey, and various shore and freshwater birds. It is likely that additional animal species were similarly impacted, including a substantial loss of amphibians, reptiles and invertebrates. Consequently, Polynesian settlement on Banks Peninsula may have been responsible for local disruptions in various ecosystem processes, such as complex food webs, gene flows and regeneration dynamics.

A few decades after Captain James Cook and his crew first sighted Banks Peninsula in 1770, some European flax traders, sealers, and whalers, began to land regularly on its coasts, enabling the introduction of the European rat (*Rattus norvegicus*) into the region. Within half a century, European colonisers cleared the vast majority of the Peninsula's forests, by converting the land into pasture, exploiting timber, milling, and inadvertently or purposely inducing fires. By 1920, the original forest cover on Banks Peninsula had been almost completely removed, only remaining as small isolated remnants in steep gullies (Figure 1.2b). Furthermore, wetlands were dried and exotic plants and animals were introduced, causing considerable losses within the native biodiversity. It is estimated that at least 20 plant species became extinct, and as many are so rare that they are threatened with local extinction. Along with this radical habitat

destruction, the introduction of exotic predators, including rats, hedgehogs, cats, ferrets, stoats, and the competition for food with exotic birds and mammals, resulted in the local loss of 26 native bird species, mainly parrots and forest birds. A notable number of introduced birds, mammals, fish, amphibians and invertebrates have fully naturalised, potentially replacing extinct native species in food chains, species interactions and other ecosystem niches. "Nevertheless", as Wilson (2013) points out, "exchanging kokako for sparrows, piopio for starlings, or kakariki for magpies, is not much of a swap." Indeed, the contribution of exotic birds to pollination and seed dispersal of native plants is very limited, accounting for only about 5% of all bird visits to native flowers and fruits (Kelly et al. 2006).

Since the early 20th century, a significant proportion of the open pasture has now reverted to native trees and shrubs, and to exotic scrubs of gorse and broom that can facilitate the regeneration of forest plant species. Fragments of old growth forests are extremely scarce on Banks Peninsula, covering less than 1000 ha or 1% of their pre-Maori range. Nonetheless, the gradual regrowth of native tree species for the past century has led to the current extent of 15% native bush (Figure 1.2c). Yet, an equivalent proportion of the land is now covered with exotic plantations, and two thirds of Banks Peninsula's vegetation cover is still made of grassland, including a majority of exotic species, grazed on by stock, and mostly depleted of native birds.

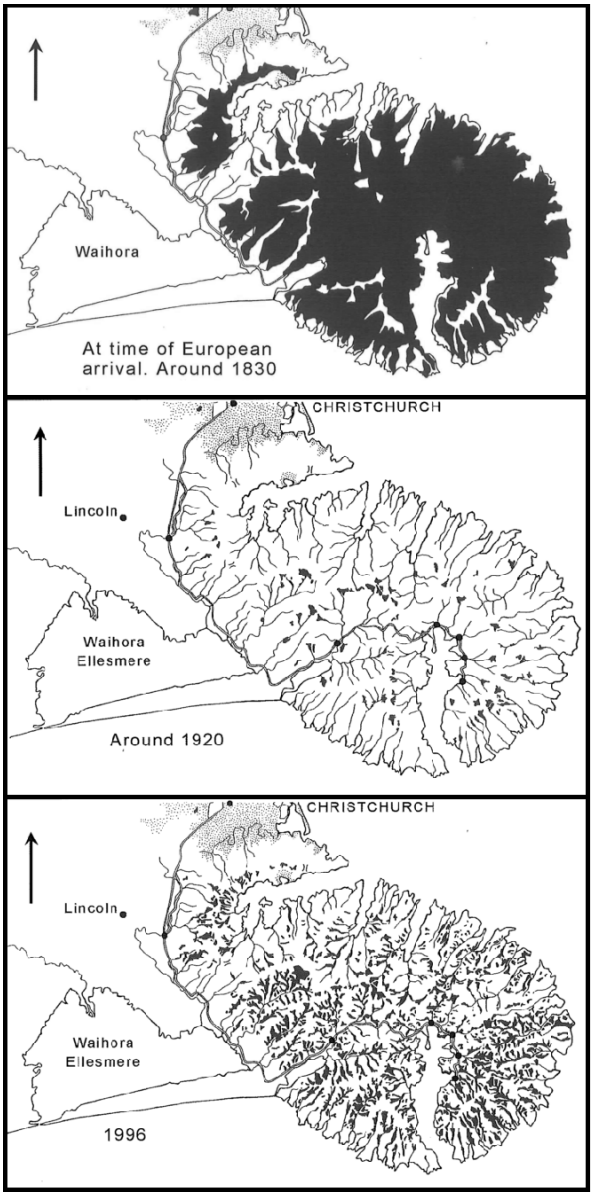

Figure 1.2: Estimated native forest cover on Banks Peninsula, (a) around 1930, just prior European settlement, (b) around 1920, after the end of milling, and (c) in 1996, current extent of regenerating forest (Wilson 2013)

V. Thesis outline

The overall aim of this thesis is to investigate the effectiveness of pollination and dispersal mutualisms by birds in the context of forest fragmentation. To address this issue, I follow the fragmented population of a bird-pollinated, bird dispersed tree along its main stages of reproduction.

A decrease in mutualist density can be responsible for the disruption of plant-bird mutualisms (Holdaway 1989; Thorsen et al. 2009). Habitat fragmentation and changes in biodiversity both have an influence on birds' foraging behaviours and competition mechanisms, which in turn can result either on positive or negative effects on pollination or dispersal service, with consequences on plant recruitment (Kearns et al. 1998; Lennartsson 2002; Mustajarvi et al. 2001; Quesada et al. 2003; Quesada et al. 2004; Burgess et al. 2006; Herrera & Garcia 2010; Robertson et al. 2011). In Chapter 2 I gather biotic and abiotic data to characterize the environmental factors of 18 study sites on Banks Peninsula. Using GIS methods I generate several parameters of habitat fragmentation, including area and connectivity, while local bird densities and some descriptors of vegetation structure are estimated from field measurements and personal observations. Statistical tests allow for the identification of the site parameters with a significant effect on bird densities, which are expected to increase for the native avifauna with area and connectivity (Sekercioglu et al. 2004; Fahrig 2013).

The remainder of this thesis uses the set of site data and results from Chapter 2 to assess the effects of habitat fragmentation and mutualist bird densities on the various phases of reproduction of an indicator native plant. In Chapter 3, I begin with the evaluation of pollination service on a gynodioecious plant, based on field scores of pollen loads on hundreds of flowers. Given the ability of hermaphrodite individuals to self-pollinate, and the reliance of female plants on active pollination by birds to receive some pollen, pollination levels on hermaphrodite flowers are expected to be invariably high, whereas low pollen scores on females are an indication of poor pollination service (Robertson et al. 2008). In Chapter 4, local dispersal service is estimated using field rates of fruit removal (Robertson et al. 2008). In sites with high densities of frugivorous birds, and low levels of fragmentation, fruiting plants are expected to receive sufficient interaction with birds for an important quantity of their seeds to be ingested and potentially dispersed (Cordeiro & Howe 2003; Cramer et al. 2007; Herrera & Garcia 2010).. In Chapter 5, I explore various aspects of the recruitment success of parent trees from forest fragments: seed production, germination, and seedling growth, which can all be affected in the occurrence of inbreeding depression. In the case of insufficient pollination service, low pollen income to female flowers will result in the production of a reduced seed set, but because the

seeds are necessarily produced from outcrossing, their ability to germinate and grow into a healthy individual should remain unaffected (Robertson et al. 2011). Hermaphrodites lacking interaction with birds are able to compensate by self-pollinating, in which case their seed set shouldn't be impacted, but the selfed seeds will have reduced fitness, potentially showing low germination rates and slow seedling growth (Robertson et al. 2011). In Chapter 3, 4 and 5, I compare respectively the site-specific levels of pollination, seed dispersal, and inbreeding depression, with the local bird densities, fragmentation levels and aspects of vegetation structure determined in Chapter 2.

A genetic experiment using specific microsatellites markers was designed to assess the local genetic diversity among adult trees and the percentage of selfed individual among hermaphrodite progeny in 10 study sites, and the patterns of pollen flow in three small populations where all the adults could be sampled. An analysis testing the effects of fragmentation and bird density on these genetic data of mating patterns was planned to be presented in an additional chapter, however several technical problems resulting from equipment failures caused repeated delays and eventually prevented the experiment to be completed within the course of this PhD. Therefore, the genetic aspects of plant reproduction via bird pollination on Banks Peninsula won't be discussed further in this thesis.

Finally, in Chapter 6 I synthesize the main findings from each chapter in a summary of the effects of each site descriptor on bird densities and plant-bird interactions in my study area, and how they compare with results from other studies in New Zealand and worldwide. Based on these results, I emphasize the implications for conservation practice in fragmented landscapes, including some recommendations for the preservation or the restoration of plant-bird mutualism in forest fragments.

CHAPTER 2:

Lowland forest fragmentation and bird communities on Banks Peninsula

Kereru (Hemiphaga novaeseelandiae), a native frugivore and important seed dispersor, sitting on a branch in Hay Scenic Reserve, Banks Peninsula

(Photo Marine Aubert)

I. Introduction

Forest fragmentation is characterized by the reduction in area and increase in isolation of forested patches, both causing significant declines in plant and animal communities (Wilcox & Murphy 1985; Ewers & Didham 2006; Mortelliti et al. 2010). As a result of habitat destruction, and introduction of exotic predators and competitors, losses in native biodiversity may lead to local alterations of ecosystem dynamics, including mutualistic interactions. Decreases in species richness and abundance among the guild of mutualists affect breeding success, dispersal, and foraging behaviours of pollinators and seed dispersers (Kurtis Trzcinski et al. 1999; Fahrig 2013), potentially reducing gene flows between isolated plant populations, eventually leading to seed-limitation, and regeneration failures (e.g. Rathcke & Jules 1994; Steffan-Dewenter & Tscharntke 1999; Robertson et al. 1999; Quesada et al. 2004; Harris & Johnson 2004; Herrera & Garcia 2010). Nevertheless, some of the changes in habitat configuration conveyed by forest fragmentation can have positive effects on mutualist immigration rates and mutualism success (Burgess et al. 2006; Lander et al. 2010).

Forest conversion into agricultural land can allow for an increase in total biodiversity, with the integration of introduced biota into the modified trophic chain, providing alternative food sources and competing for original resources (Andren 1994; Deconchat et al. 2009; Barbaro et al. 2012). An increase in edge surface has been shown to intensify species movements and modify the stability of species interactions, a phenomenon referred to as the "hyperdynamism" of habitat edges in fragmented landscapes (Ewers & Didham 2006). The positive or negative response of a species to habitat fragmentation depends on the species degree of specialization and life history traits: generalist species are likely to take advantage of changes in environmental structure and biodiversity, whereas highly specialized, territorial species may struggle to adapt to the biotic and abiotic alterations of their original habitat (Andren 1994; Ewers & Didham 2006; Fahrig 2013).

Since human settlement in New Zealand, native lowland forests have been highly fragmented, now mainly remaining as small patches surrounded by exotic grassland or tree plantations (Walker et al. 2008). Following habitat loss and introduction of mammalian predators, the considerable decline in native land bird populations is of particular concern for the large number of native forest plants that rely on birds for pollination and seed-dispersal: about one third of the native woody basal area is made of plants whose fruits or flowers are visited by birds at least occasionally (Kelly et al. 2010). Moreover, almost all birds involved in mutualism with indigenous plants are native species: Kelly et al. (2006) found that bellbird, tui, silvereye, and range-limited stitchbird were together responsible for over 90% of all visits to

the flowers of 18 native species throughout the country, and about 85% of fruit consumption by birds on 32 native plant species was carried out by bellbird, tui, silvereye, kereru and the rare saddleback (present at one study site only). No exotic species was found to participate notably in native plants' pollination, but the introduced blackbird was the main exotic contributor to frugivory (3.9% of all visits to native fruits, Kelly et al. 2006).

In the context of forest fragmentation, species movements and increased competition induced by the modifications in vegetation structure are likely to affect densities and distributions of all bird species, therefore affecting key ecological processes, such as mutualist interactions with plants and rates of predation on invertebrates. Banks Peninsula's original forest cover has been highly fragmented: its landscape is now scattered with many small forest patches. In a study comparing bird assemblages at the edge and in forest interiors of native forest remnants on Banks Peninsula, Barbaro et al. (2012) found significantly higher species densities and diversity at forest edges, where exotic species were dominant, whereas native species were more abundant in forest interiors, regardless of patch area. In an earlier study on Banks Peninsula, Deconchat et al. (2009) showed that although native bird densities were higher in native forest patches, native birds were also present to some extent in exotic tree plantations, and in minor numbers within farmland plots. As forest fragmentation causes movements of native forest birds to complementary resources within the surrounding agricultural matrix, and the immigration of exotic bird species into native forests, it is not known how site-specific fragmentation parameters are influencing bird communities in forest remnants. Do mutualist birds remain in sufficient numbers in small forest fragments to ensure efficient pollination and seed dispersal services to native plants? Can connectivity compensate for the reduction in habitat area in maintaining adequate abundance of mutualist birds? Which native bird species are the most affected by forest fragmentation?

In New Zealand, bird densities are usually estimated using a standard 5-min bird count method. This technique was developed in the early 1970s, when no specific method was recognized in the country or globally as most suitable for the estimation of local bird communities (Hartley 2012). Several methods based on plot or transect counts, including Emlen's (1971) distance sampling, have been used in various studies but without general consensus (Dawson & Bull 1975; Hartley 2012). Distance sampling is not ideal in New Zealand because most forest birds are detected audibly rather than by sight; the estimation of their distance to the counting transect is subjective, and varies between observers. Moreover, the conspicuousness of birds is affected by the presence of people, some species tending to get attracted or to move away from people, and some remaining silent and hardly detectable even when perched nearby the observer (Dawson & Bull 1975). In a comparative study, Dawson &

Bull (1975) tested three standardized bird count techniques: walking counts (an observer counts all birds seen or heard while slowly walking along a track), 5-min counts (an observer counts all birds seen or heard while standing still for 5 minutes at a fixed station, at several stations distant by about 200 m from each other) and 10-min counts (similar to 5-min counts but with counts lasting for 10 minutes). They found very little variation in estimated local bird densities between the three techniques, however fixed counts were favoured because counts in motion could decrease the attention of the observer to the birds and be affected by topographical changes. Five and ten minute counts were both as accurate, but shorter counts allowed for more sampling occurrences within the same amount of time and decreased the odds of counting an individual bird more than once (Dawson & Bull 1975). This standard 5-min count has since been accepted and widely used for over 40 years throughout New Zealand, where it has been included in over 260 published studies (Hartley 2012); it is the method used to estimate bird densities in the present study.

In this chapter I assess bird densities in several native forest fragments varying in altitude, area, shape complexity, and connectivity level. I compare fragmentation parameters commonly used in landscape ecology studies to identify useful indices that can be easily measured, and are relevant to New Zealand's fragmented landscape of lowland forest remnants embedded in a pastoral matrix. Using a simple set of measures, I aim to determine which fragmentation variables have a significant effect on the abundance of native and exotic birds in lowland forest patches, especially mutualist bird species.

II. Methods

Study sites

Field work was conducted at 18 sites on Banks Peninsula (Figure 2.1). The criteria used to select these study sites were their location (i.e. within the Herbert or Akaroa districts of Banks Peninsula ecological region, Wilson 1992), status (i.e. conservation lands, officially recognized for their ecological value), accessibility (land owners or managers gave permission to carry out field work on site), comparability of vegetation structure (i.e. native remnants of mixed broadleaf/podocarp forests), absence of browsing by stock (all sites were fenced off, however there was evidence of wild deer presence at some locations), and variation in size and distance to neighbouring forested patches.

Ten sites were scenic reserves managed by the Department of Conservation (DOC), the other eight were private open-space covenants managed by Queen Elizabeth II National Trust (six sites), Maurice White Native Forest Trust (one site), and Banks Peninsula Conservation Trust (one site). The level of management of possum and rats varied greatly between sites, ranging from no management to considerable pest control measures, such as trapping and poisoning (Table 2.1).

Table 2.1: Land status, management body, vegetation type and current pest control measures in 18 lowland forest patches on Banks Peninsula (ordered alphabetically).

Site	Status	Management	Vegetation	Current pest control (possum)
Blind Bay	Private covenant	QEII Nat. Trust	Dryland podocarp-hardwood forest	Perimeter toxic baits
Cloud Farm	Private covenant	QEII Nat. Trust	Mixed tōtara-hardwood forest	NA
Hay	Scenic Reserve	DOC	Podocarp forest	Goodnature traps
Hinewai	Private covenant	M. White Native Forest Trust	Mixed beech-podocarp-broadleaf	Trapping, shooting and poisoning
Kaituna	Scenic Reserve	DOC	Podocarp forest	Perimeter trapping
Magnet Bay	Scenic Reserve	DOC	Mixed podocarp-hardwood forest	None
Montgomery	Scenic Reserve	DOC	Mixed conifer-hardwood forest	None
Mt Pearce	Scenic Reserve	DOC	Mixed tōtara-broadleaf forest	None
Mt Sinclair	Scenic Reserve	DOC	Mixed tōtara-broadleaf forest	Perimeter toxic baits (Feratox) 2013-15
Oashore	Private covenant	QEII Nat. Trust	Mixed podocarp-hardwood forest	Goodnature Traps (possum and rats)
Otepatotu	Scenic Reserve	DOC	Mixed podocarp-hardwood forest	Perimeter trapping
Pearce QEII	Private covenant	QEII Nat. Trust	Mixed podocarp-hardwood forest	NA
Prices Valley	Private covenant	BPCT Nat. Trust	Mixed podocarp-hardwood forest	None
Tipperary Bush	Private covenant	QEII Nat. Trust	Mixed conifer-hardwood forest	Occasional shooting in the area
Tipperary Gully	Private covenant	QEII Nat. Trust	Mixed conifer-hardwood forest	Occasional shooting in the area
Tutakakahikura	Scenic Reserve	DOC	Red beech forest	None
Waghorn	Scenic Reserve	DOC	Mixed tōtara-broadleaf forest	Perimeter toxic baits (Feratox) 2013-15
Whatarangi	Scenic Reserve	DOC	Mixed tōtara-broadleaf forest	Perimeter toxic baits (Feratox) 2013-15

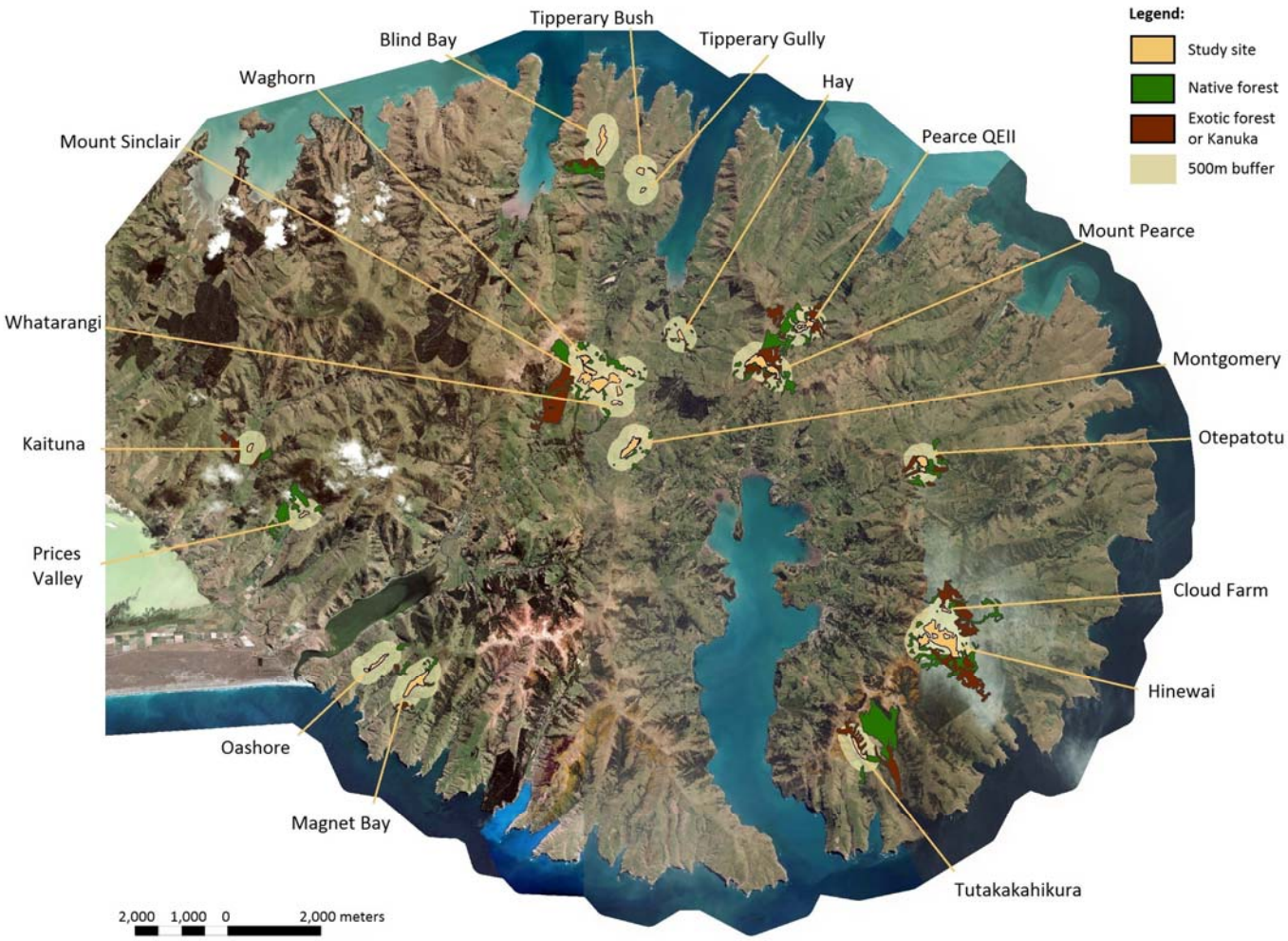

Figure 2.1: Location of the 18 study sites on Banks Peninsula and their neighbouring forested patches with a boundary within 500 m of the edge of the sites, included in the calculation of connectivity indexes. Map created with ArcGIS 10.3.1, aerial orthophoto 2010 (source Creative Commons Attribution 3.0 New Zealand)

Fragmentation parameters

In empirical literature, the parameters describing habitat fragmentation include up to five distinct spatial metrics of individual patches in fragmented landscapes: matrix structure, patch area, patch shape, edge effects, and fragment connectivity (Ewers & Didham 2006).

- In my study, the nature of the surrounding **matrix structure** did not differ between sites: all forest fragments were embedded in farmland, typically hill country grazed pasture. Only six sites (Cloud Farm, Hinewai, Magnet Bay, Mount Pearce, Pearce-QEII, and Tutakakahikura) shared some boundaries with adjoining patches of exotic woodland such as pine tree plantations.

- Using the geospatial software ArcGIS© version 10.3.1 by ESRI Inc., I calculated the actual **forested area** of each site (Table 2.2) by creating accurate forest patch polygons, adjusted from cadastral boundaries after thorough comparison to Landcare Research's Land Cover DataBase version 2 (LCDB2) and to recent aerial orthophotos (from 2010) of Banks Peninsula region.

- As the complexity of a **patch shape** increases, the extent of its core area decreases: long, sinuous and narrow fragments have proportionally less core area than a circular patch of similar area. Calculated as an edge ratio, patch shape gives an indirect estimation of the extent of local **edge effect**, which has been associated with the dominance of exotic bird species and hyperdynamism of ecological processes (Ewers & Didham 2006; Barbaro et al. 2012). At the landscape level, convoluted shapes may have a greater visibility to disperser species than compact fragments (Rutledge 2003; Yamaura et al. 2008). For each study site, I calculated two common shape measures (Table 2.2): the perimeter to area ratio $PARA_i = p_i/a_i$, and Shape Index SI (Patton 1975), which measures the deviation of a patch shape to circularity independently from patch area, dividing patch perimeter by the perimeter of a circle of identical area: $SI_i = p_i/2\sqrt{\pi a_i}$. In both equations, p_i is the perimeter (in m) of patch i, and a_i is its area (in m^2).

PARA and SI were not correlated with each other, but were both highly correlated with area, in opposite directions (Figure 2.2). The correlation of SI with area was unexpected, as unlike PARA it is a measure specifically designed to be independent from area. This correlation indicates that among the set of sites used in this study, larger patches also happened to have more complex shapes, whereas small patches had simpler forms. Tested in generalized linear models to assess their effect on bird densities, both indices showed similar effects, and were usually removed by stepwise analyses. Therefore, neither measure of patch shape was included in the following analyses.

- **Connectivity** is a relative measure that is specific to the organisms involved and the scale of their movements between habitat patches. As this study focuses on plant-bird interactions, site connectivity was calculated in relation to neighbouring patches that could be considered as "suitable habitats" for the regeneration of *Fuchsia excorticata* and/or for providing resources to mutualist birds, such as food sources or breeding territories.

I assessed all LCDB2 cover types (Thompson et al. 2003) for their suitability in order to exclude all inappropriate classes. The land cover classification is structured into seven primary classes: artificial surfaces, bare or lightly vegetated surfaces, water bodies, cropland,

grassland/sedgeland/saltmarsh, scrub and/or shrubland, and forest. The first five categories were considered as unsuitable and were not included in the connectivity calculation. I kept a selection of subdivisions of the scrub and/or shrubland, and forest classes:

- "Manuka and/or Kanuka": an early successional scrub type on formerly forested area, with advanced stage of reversion indicated by the presence of mature stands and broadleaved forest species. On Banks Peninsula this is nearly all kanuka (*Kunzea ericoides*).
- "Broadleaved Indigenous Hardwoods": an advanced successional stage back to indigenous forest, typically ranging from 3 to 10 m in canopy height and usually located in high rainfall areas in hill country, characterised by the presence of a mix of broad-leaved, generally seral hardwood species, including *Fuchsia excorticata*, mahoe (*Melicytus ramiflorus*), *Pseudopanax* spp., *Pittosporum* spp., ngaio (*Myoporum laetum*), and titoki (*Alectryon excelsus*).
- "Forest - Harvested", "Pine Forest - Open Canopy", "Pine Forest - Closed Canopy", and "Other Exotic Forest" include harvested pine forests that are being replanted, indigenous or exotic forests converted to another land cover, recent (6 to 15 years old) and advanced (over 15 years old) *Pinus radiata* plantations, stands of wilding pines, and exotic forests consisting of conifers other than *Pinus radiata* or evergreen broad-leaved species.
- "Deciduous Hardwoods", including willow and poplar species growing along rivers and waterways, and stands of planted exotic deciduous hardwoods.
- "Indigenous Forest", defined as vegetation dominated by indigenous tall forest canopy species.

The geospatial analysis identified within the study area (i.e. Herbert and Akaroa Ecological Districts) a total of 2,681 "suitable patches", including the 18 study sites, that together were covering 15,744 ha, roughly 18% of Banks Peninsula's land area.

Studies on New Zealand native land bird movements are limited, and have shown that large mutualist birds, such as kereru and tui, are capable of long distances flights, reportedly up to 33 km between native forest stands (Stewart & Craig 1985; Clout et al. 1991; Powlesland et al. 2011). At that scale, no forest fragment on Banks Peninsula could be considered as completely isolated. Using radio telemetry techniques, Spurr et al. (2010) found that bellbird, the main pollinator and important seed disperser of *F. excorticata*, but also a territorial bird, had an estimated average home-range of 0.7 to 0.9 ha per pair. Most movements of bellbirds across farmland between forest patches, from their core home range to patchy food sources, were shorter than 200 m, but occasionally exceeded 500 m (Spurr et al. 2010). Therefore, I used

500 m as the threshold distance around study sites to calculate their connectivity levels: among the 2,681 "suitable patches", there were a total of 126 sites with a boundary contained within the 500 m buffers created with ArcGIS around all 18 study sites.

As landscape connectivity has widely proven a vital factor in preventing local population decline, and allowing essential dispersal processes and gene flows between natural habitats, many geospatial network indices have been developed and compared in several reviews. However, no single index clearly appeared to be the most practical in habitat fragmentation analyses, so I chose to test four different connectivity indexes on the Banks Peninsula landscape, all recommended by various authors as the "best" binary or probabilistic index to describe the whole landscape connectivity (e.g. Jordán et al. 2003; Pascual-Hortal & Saura 2006; Saura & Pascual-Hortal 2007; Bodin & Saura 2010; Baranyi et al. 2011; Ernst 2014):

- **Harary index**: $H = \frac{1}{2}\sum_{i=1}^{n}\sum_{j=1,i\neq j}^{n}\frac{1}{nl_{ij}}$ where n is the total number of suitable patches in the landscape, and nl_{ij} is the number of links in the shortest path (topological distance) between patches i and j. For patches that are not connected $nl_{ij} = \infty$.
- **Landscape Coincidence Probability**: $LCP = \sum_{i=1}^{NC}\left(\frac{c_i}{A_L}\right)^2$ where NC is the number of components (i.e. groups of connected patches) in the landscape, c_i is the total component area (i.e. sum of the areas of all the patches belonging to that component), and A_L is the total landscape area (including both habitat and non-habitat patches).
- **Integral Index of Connectivity**: $IIC = \frac{\sum_{i=1}^{n}\sum_{j=1}^{n}\frac{a_i \cdot a_j}{1+nl_{ij}}}{A_L^2}$ where n is the total number of patches in the landscape, a_i and a_j are areas of patches i and j, nl_{ij} is the number of links in the shortest path (topological distance) between patches i and j, and A_L is the total landscape area. For patches that are not connected the numerator in the equation for IIC equals zero ($nl_{ij} = \infty$). When i = j then $nl_{ij} = 0$.
- **Probability of Connectivity**: $PC = \frac{\sum_{i=1}^{n}\sum_{j=1}^{n} a_i \cdot a_j \cdot p_{ij}^*}{A_L^2}$ where n is the total number of patches in the landscape, a_i and a_j are the areas of patches i and j, and A_L is the total landscape area. p_{ij}^* is the maximum product probability of all paths between patches i and j. If patches i and j are close enough, the maximum probability path is a unique step from patches i to j ($p_{ij}^* = p_{ij}$). If patches i and j are distant, the maximum probability path will comprise several steps ($p_{ij}^* > p_{ij}$). When two patches are isolated from each other by a too long distance or by a land cover feature preventing movement between both patches, then $p_{ij}^* = 0$. When i = j then $p_{ij}^* = 1$.

I used the free software Conefor version 2.6 developed in Universidad Politécnica de Madrid, Spain (Saura & Torne 2012) to generate these four connectivity indices for Banks Peninsula. Conefor calculated the importance of each patch (dI) within the fragmented landscape for preserving the current state of connectivity given a certain index (I). This individual patch connectivity measure was calculated as a percentage using: $dI(\%) = 100 \cdot \frac{I - I_{remove}}{I}$ where I was the overall landscape index value (H, LCP, IIC, or PC) when all suitable patches (i.e. 18 study sites plus 126 neighbouring patches) were taken into account, and I_{remove} was the new landscape index value after the virtual loss of that distinct habitat patch from the landscape. For each patch, Conefor generated an individual dH, dLCP, dIIC, and dPC value.

dLCP, dIIC and dPC were highly correlated with each other, but less with dH (Figure 2.2), which also had the advantage of being independent from patch area. All four parameters were tested in generalized linear models to assess their effect on bird densities, pollination and dispersal, and models using dH always had a lower AIC and stronger effects. Therefore, I chose dH as the sole landscape-scale fragmentation parameter to use in all analyses (Table 2.2).

As dH is a connectivity measure derived from the overall connectivity of the network of patches across the study area, I also calculated two site-specific connectivity indices that only used the geographical characteristics of each patch and its immediate neighbourhood (Moilanen & Nieminen 2016):

- **Area to distance ratio** $ADRA_i^x$ sums up the ratios of area to weighted distance to each neighbouring "suitable patch" j within 500 m of study site i: $ADRA_i^x = \sum_{j=1}^{n} \frac{a_j}{(l_{ij})^x}$ where n is the total number of suitable patches, a_j is the area of neighbouring patch j in hectares, and l_{ij} is the shortest path (topological distance in meters) between patches i and j, weighted by exponent x. I compared several ADRA values varying in distance weight x, using squared distance (x = 2), unweighted distance (x = 1) and root squared distance (x = 0.5). All were highly correlated with each other and produced similar effects in generalized linear models, which had a lower AIC when using x = 1. Therefore, I used $ADRA_i^1$ in all following analyses (Table 2.2).
- **Hanski's (1994) Incidence Function Measure:** $IFM_i = \sum_{j \neq i}^{n} e^{(-\alpha l_{ij}) a_j^{0.25}}$ uses a negative exponential dispersal coefficient scaled on α (the inverse of the average migration distance d) where α =1/d (here d = 500 m, so α = 0.002); n is the total number of suitable patches within 500 m around patch i, a_j is the area of neighbouring patch j in hectares, and l_{ij} is the shortest path (topological distance in meters) between patches i and j.

ADRA and IFM were highly correlated with each other, and both were also moderately correlated with Area and with dH (Figure 2.2). The two parameters were tested in linear mixed models to assess their effect on bird densities. The models alternatively resulted in stronger effects or had a lower AIC when using one or the other, but backward stepwise analyses removed IFM from all models. Therefore, I chose ADRA as the sole patch-scale fragmentation parameter to use in all analyses (Table 2.2).

- **Altitude** is not a fragmentation parameter, but it is an environmental variable known to affect bird distributions. As most sites were located on slopes within an altitudinal range from top to bottom, I located in ArcGIS the centroid of each site polygon on a topographic map of Banks Peninsula and rounded its elevation to the closest 20 m line. I used the exact altitude (rounded to the nearest 5 m) for the 3 reserves lower than 50 m: Hay, Kaituna and Prices Valley (Table 2.2). These rounded altitudes per site were used in the analyses of pollination, seed dispersal and inbreeding depression, whereas bird counts were analysed using the actual altitude (rounded to the nearest 20 m) of each count station.

Table 2.2: Fragmentation measures of 18 lowland forest patches on Banks Peninsula (ordered alphabetically), including altitude, area, shape indices (PARA and SI), and connectivity indices (dH, dLPC, dIIC, dPC, ADRA and IFM).

Site	Alt. (m)	Area (ha)	PARA (m^{-1})	SI (m^{-1})	dH (%)	dLCP (%)	dIIC (%)	dPC (%)	ADRA ($ha.m^{-1}$)	IFM
Blind Bay	360	20.66	1.31	1.68	0.26	0.404	0.377	0.371	0.27	3.70
Cloud Farm	620	4.05	2.65	1.50	1.88	0.397	0.451	0.375	1.60	13.79
Hay	35	6.37	1.76	1.25	0.95	0.030	0.029	0.030	0.12	8.12
Hinewai	400	93.44	0.97	2.66	4.39	8.276	7.294	8.349	7.48	21.42
Kaituna	10	5.34	1.80	1.17	0.40	0.552	0.470	0.466	0.15	4.72
Magnet Bay	240	29.49	1.19	1.83	1.21	0.624	0.529	0.560	0.77	7.69
Montgomery	500	23.38	1.18	1.60	0.50	0.257	0.261	0.256	0.13	4.74
Mt Pearce	540	38.07	1.19	2.08	1.32	3.202	2.368	3.318	3.77	14.42
Mt Sinclair	740	74.72	1.20	2.91	6.40	6.068	5.722	6.665	1.01	15.30
Oashore	240	12.87	2.28	2.31	1.08	0.463	0.209	0.274	0.03	1.75
Otepatotu	660	16.84	1.31	1.51	1.00	0.373	0.335	0.380	2.30	13.98
Pearce QEII	240	18.58	2.02	2.46	1.45	1.601	1.122	1.659	6.61	16.71
Prices Valley	40	5.09	2.23	1.42	0.31	0.104	0.088	0.094	0.39	5.64
Tipperary Bush	380	6.09	1.63	1.13	0.16	0.011	0.012	0.010	0.02	1.39
Tipperary Gully	300	2.84	2.61	1.24	0.09	0.006	0.005	0.004	0.01	0.60
Tutakakahikura	380	12.89	1.97	1.99	0.44	0.786	0.667	0.949	2.57	7.92
Waghorn	680	8.60	1.55	1.28	1.69	0.758	0.518	0.735	1.53	8.88
Whatarangi	580	5.22	2.04	1.31	1.27	0.462	0.279	0.390	0.43	3.88

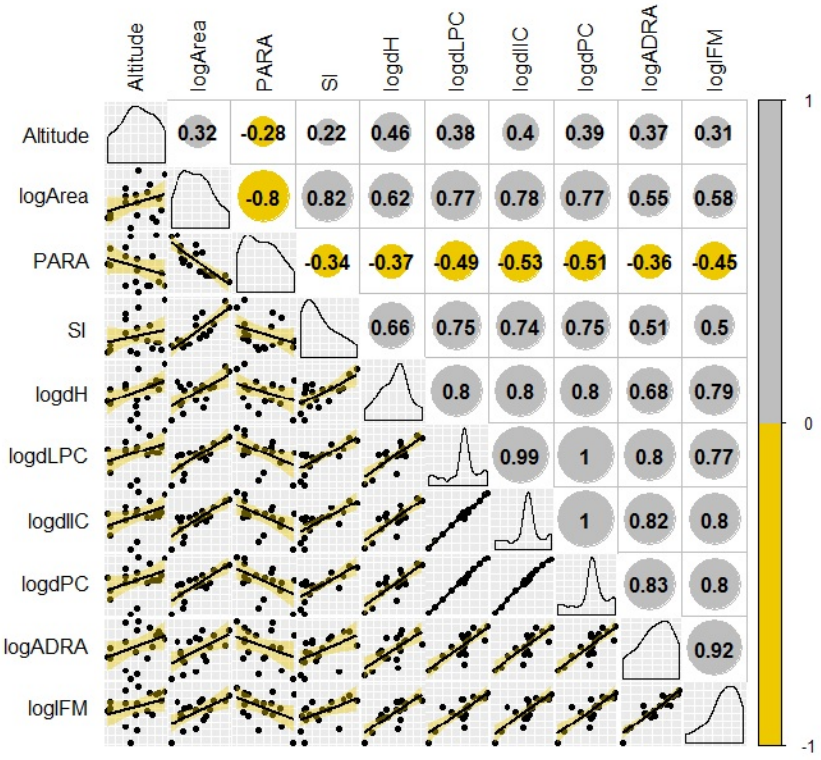

Figure 2.2: Matrix of Pearson's correlation coefficients (upper half) and pair plots with GLM regression lines (lower half) between topographical measures of 18 lowland forest patches on Banks Peninsula.

Bird counts

Relative bird density was estimated in 18 sites using repeated standard 5-min bird counts, a method described by Dawson & Bull (1975). In total, 527 bird counts were collated: 390 counts collected during this study from two consecutive seasons of fieldwork (spring/summer 2013-14 and 2014-15), during which I had the occasional help of field assistants who did 194 counts in total, and later counts (spring 2016) all done by myself at sites with few data, plus 137 additional counts from previous surveys by ECan, M. Lettink (in Oashore), and E. Brockerhoff (used in Deconchat et al. 2009; Barbaro et al. 2012) covering the 2005-12 period (Table 2.3). All bird species detected during the counts were recorded at each site (see Table 2.6 in Result section). Because of the various sources of bird count data, there was a total 142 fixed count stations, some of which that were only used once, and some located very close to each other. Count locations were therefore assigned to block areas within each site, the smallest sites accounting for one block. In order to allow for data structure, count location was taken into account in the statistical models as a random term of block nested within site.

Table 2.3: Number of 5 min bird counts carried out in 18 lowland forest sites on Banks Peninsula, over the 2005-16 period. Those before 2013 were provided by others (see text).

Year		**2016**	**2014-15**	**2013-14**	**2012**	**2007-11**	**2006**	**2005**	
Season		Last	Second	First	Old	Old	Old	Old	
Site	**Blocks**								**Total**
Blind Bay	2			9					**9**
Cloud Farm	1	12	3	2					**17**
Hay	3		1	21	4	25		2	**53**
Hinewai	4			35		38		5	**78**
Kaituna	2			29	1	1		2	**33**
Magnet Bay	1	12	2	3					**17**
Montgomery	4		17	13	4	16		2	**52**
Mt Pearce	1	12	1			4			**17**
Mt Sinclair	2	13	2	1				8	**24**
Oashore	3		32	30	10				**72**
Otepatotu	3		5	25		2			**32**
Pearce-QEII	2			25					**25**
Prices Valley	2		7	23		2	1	2	**35**
Tipperary Bush	1			6					**6**
Tipperary Gully	1	12	1	4					**17**
Tutakakahikura	2		1	5		5			**11**
Waghorn	1	11						1	**12**
Whatarangi	2	8	2	5		2			**17**
Total		**80**	**74**	**236**	**19**	**95**	**1**	**22**	**527**

Statistical analyses

All statistical analyses were performed using the program R version 3.1.1 (R Core Team 2014). I used a generalized linear mixed model (GLMM) with Poisson error distribution (*lme4* package in R) analysed with an ANOVA based on Chi-squared test (*Anova* command from *car* package in R) to test whether count season (i.e. "first" for 2013-14, "second" for 2014-15, "last" for 2016, and "old" for previous counts) had an effect on the number of birds detected per count, for each species, across all sites (Table 2.4).

I used the formula: *glmer(formula = y ~ Site + Season + (1|Site/Block), family = poisson),* where y was the number of birds in a few common species detected per 5-min count: bellbird (the main pollinator bird on banks peninsula), blackbird (the only exotic species in the guild of mutualist birds), and rifleman (a less common endemic insectivorous forest bird).

Table 2.4: Analyses of deviance table from the generalized linear mixed models assessing the effect of site and season of bird count on the number of bellbird, blackbird, and rifleman detected per 5-min count. Bold p-values indicate a significant effect ($p < 0.05$).

Response variable	Parameter	Df	Chi-sq	p(>Chi-sq)
Bellbird	Site	17	86.6718	**< 0.001**
	Season	3	8.8908	**0.031**
Blackbird	Site	17	54.0513	**< 0.001**
	Season	3	5.6659	0.129
Rifleman	Site	17	35.7729	**0.0049**
	Season	3	5.4829	0.140

The effect of site on the number of bellbirds, blackbirds, and riflemen was highly significant ($p < 0.001$), but the effect of season had a weaker statistical significance ($p > 0.01$) for bellbird and no effect on blackbird and rifleman (Table 2.4). This indicates that across all sites, the number of birds varied greatly between sites, but not so much within sites between years: site-specific counts were apparently relatively consistent throughout the years.

To investigate in more detail a possible linearity and its eventual direction in local changes in bird counts across time from 2005 to 2016, and across all sites, I tested the effect of the year of count both as a numerical parameter and as a factor using Poisson GLMMs, calling the formulas: *glmer(formula = y ~ Site + Year + (1|Site/Block), family = poisson),* and *glmer(formula = y ~ Site + as.factor(Year) + (1|Site/Block), family = poisson),* where y was the number of birds in the same three species detected per 5-min count (Table 2.5).

Table 2.5: GLMM summary and analyses of deviance table showing the effect of site and year of bird count as a categorical factor (fact.) and as a numerical parameter (num.) on the number of bellbird, blackbird, and rifleman detected per 5-min count. Bold p-values indicate a significant effect ($p < 0.05$).

Response variable		Parameter		Df	Chisq	p(>Chisq)
Bellbird	Anova outputs	Site		17	90.714	**< 0.001**
		Year (num.)		1	3.477	0.062
		Site		17	88.625	**< 0.001**
		Year (fact.)		7	28.615	**< 0.001**
	GLMM Summary	Parameter	Coef.	St. error	Z	p-value
		Year (num.)	-0.023	0.012	-1.865	0.062
		Year 2006	-1.065	1.016	-1.048	0.294
		Year 2009	0.143	0.162	0.883	0.377
		Year 2012	-0.483	0.238	-2.031	**0.042**
		Year 2013	-0.151	0.156	-0.968	0.333
		Year 2014	-0.007	0.173	-0.042	0.967
		Year 2015	0.322	0.220	1.467	0.142
		Year 2016	-0.202	0.181	-1.121	0.262
Blackbird	Anova outputs	Parameter		Df	Chisq	p(>Chisq)
		Site		17	63.790	**< 0.001**
		Year (num.)		1	0.094	0.759
		Site		17	48.020	**< 0.001**
		Year (fact.)		7	21.482	**0.003**
	GLMM Summary	Parameter	Coef.	St. error	Z	p-value
		Year (num.)	-0.006	0.019	-0.307	0.759
		Year 2006	-0.071	0.742	-0.096	0.923
		Year 2009	-0.856	0.219	-3.904	**< 0.001**
		Year 2012	-0.278	0.317	-0.874	0.382
		Year 2013	-0.365	0.193	-1.895	0.058
		Year 2014	-0.682	0.245	-2.785	**0.005**
		Year 2015	-0.652	0.454	-1.435	0.151
		Year 2016	-0.409	0.243	-1.684	0.092
Rifleman	Anova outputs	Parameter		Df	Chisq	p(>Chisq)
		Site		17	35.612	**0.005**
		Year (num.)		1	0.538	0.463
		Site		17	34.944	**0.006**
		Year (fact.)		7	7.696	0.360
	GLMM Summary	Parameter	Coef.	St. error	Z	p-value
		Year (num.)	-0.003	0.004	-0.734	0.463
		Year 2006	0.989	3.12e05	0.000	1.000
		Year 2009	0.730	0.5796	1.260	0.208
		Year 2012	-16.708	6.65e04	-0.002	0.998
		Year 2013	0.777	0.5419	1.434	0.152
		Year 2014	0.048	0.7047	0.068	0.946
		Year 2015	0.980	9.11e04	0.000	1.000
		Year 2016	-0.323	0.5076	-0.637	0.524

The analysis revealed a significant variation in bellbird and blackbird densities between years, but this variation wasn't linear across time (year (num.) terms). For bellbird and blackbird, most years were not significantly different in bird abundance than the others, and there was no significant difference between any given years in rifleman densities (Table 2.5). This random temporal variation may be attributable to the data structure (i.e. variable amount

of bird counts each year between sites, with no count some years in several sites), to local changes in bird communities in reaction to temporary biotic or abiotic factors (e.g. short-term predator control in some reserves), or to environmental conditions affecting bird detection on the particular days of the counts (e.g. wind noise, cloud, hour of the day).

As bird densities were not significantly increasing or decreasing over time, I assumed that the effects of forest fragmentation on bird communities were consistent, and that no other major factor had affected local bird abundances in the study sites across the past decade. Therefore, all count data available from 2005 for the 18 study sites were used in the analyses, where count year as a categorical factor was included as a random term so that the temporal variation was taken into account.

To test the effect of forest fragmentation on bird densities, four topographical variables (station altitude, patch area, landscape-scale connectivity index dH, and patch-scale connectivity index ADRA) were introduced as fixed terms in generalized linear mixed models (*glmer* command in R package *lme4*) with a Poisson error distribution for count data. Area, dH and ADRA were log-transformed in order to increase the normality of their distribution across data. Altitude was normally distributed, but to maintain an appropriate scale of data between fragmentation parameters in the model it was expressed in kilometres, ranging from 0.01 to 0.76 km at 142 stations. Block nested within site, and year of count were included as random factors, to allow for data structure. I used the formula: *glmer (formula = y ~ Altitude + log(Area) + log(ADRA) + log(dH) + (1|as.factor(Year)) + (1|Site/Block), family = poisson)* where the response variable y was the number of birds in each species or group of species detected per 5-min count.

III. Results

The average number of birds detected per 5-min at each site was calculated using all data from 2005 to 2016, for the main pollinator and seed-disperser birds, some native insectivorous forest birds, and the most common exotic birds (Table 2.6).

Table 2.6: Average number of birds detected per 5 min count, at 18 lowland forest sites on Banks Peninsula, over the 2005-2016 period, including all mutualist birds, most common native and exotic birds, as individual species and/or as groups of species: total pollinators (bellbird, silvereye and tui), dispersers (bellbird, blackbird, kereru and silvereye), non-mutualist native birds (fantail, brown creeper, grey warbler, tomtit, rifleman, shining cuckoo, kingfisher, pipit, welcome swallow, spur winged plover and Australasian harrier), finches (chaffinch, goldfinch, greenfinch, yellowhammer, redpoll, and any unidentified finches), and non-mutualist exotic birds (total finches, song thrush, dunnock, magpie, Californian quail, skylark, starling, house sparrow, and sulfur-crested cockatoo).

	Mutualist birds							Common native birds						Common exotic birds		
Site	**Bellbird** *Anthornis melanura*	**Blackbird** *Turdus merula*	**Kereru** *Hemiphaga novae-seelandiae*	**Silvereye** *Zosterops lateralis*	**Tui** *Prosthemadera novae-seelandiae*	**Pollinators**	**Dispersers**	**Fantail** *Rhipidura fuliginosa*	**Brown Creeper** *Mohoua novae-seelandiae*	**Grey Warbler** *Gerygone igata*	**Tomtit** *Petroica macro-cephala*	**Rifleman** *Acanthisitta chloris*	**Non-mutualist natives**	**Song Thrush** *Turdus philomelos*	**Finches**	**Non-mutualist exotics**
Blind Bay	1.33	0.44	0	0	0	1.33	1.78	1.22	0	0.22	0	0	2.22	0.44	6.22	6.78
Cloud Farm	2.65	1.24	0.47	2.65	0.12	5.41	7.00	0.00	0.35	0.76	0.47	0.65	2.29	0.47	1.76	2.24
Hay	3.32	0.89	0.58	1.21	0	4.53	6.00	1.28	0.21	0.25	0.02	0.06	1.89	0.47	2.64	3.87
Hinewai	2.31	1.23	0.58	0.88	0	3.19	5.00	0.49	2.13	0.22	0.79	0.45	4.19	0.54	3.76	4.73
Kaituna	1.64	1.21	0.67	0.45	0	2.09	4.27	0.88	0.06	0.64	0.03	0	1.94	0.79	3.79	6.27
Magnet Bay	2.65	0.94	0.35	1.12	0	3.76	5.06	0.53	0.76	0.59	0	0.18	2.06	0.41	4.41	4.82
Montgomery	2.83	0.98	0.15	2.29	0.02	5.13	6.25	0.56	0.37	0.63	0.62	0.12	2.54	0.37	2.04	2.83
Mt Pearce	0.88	0.59	0	0.47	0	1.35	1.94	0.12	0.47	0.47	0.06	0.12	1.24	0.12	3.24	3.53
Mt Sinclair	2.08	1.08	0	2.46	0	4.54	5.63	0.38	0.46	0.79	0.29	0.42	2.33	0.38	2.54	3.13
Oashore	2.53	0.46	0.17	2.56	0	5.08	5.71	1.22	0.36	1.32	0	0	3.14	0.28	3.86	6.31
Otepatotu	1.81	1.31	0.34	0.75	0.03	2.59	4.22	0.88	0.63	0.50	0.31	0.44	2.88	0.47	4.59	5.34
Pearce QEII	3.04	1.60	0.28	0.4	0	3.44	5.32	0.60	0.08	0.20	0.64	0.32	1.84	1.52	6.96	8.68
Prices Valley	2.60	1.43	0.60	0.51	0.06	3.17	5.14	0.69	0.06	0.94	0.03	0	2.11	0.83	5.89	8.91
Tipperary Bush	0.67	0.50	0	0.00	0	0.67	1.17	2.17	0	0	0	0	2.17	0.17	5.00	5.67
Tipperary Gully	0.35	1.76	0	2.41	0	2.76	4.53	0.29	0.29	0.06	0	0	0.88	0.65	4.29	5.00
Tutakakahikura	2.09	0.45	0.64	1.91	0	4.00	5.09	1.18	0.36	0.09	0.27	0.27	2.18	0.73	3.00	4.27
Waghorn	3.25	0.58	0.08	0.58	0	3.83	4.50	0.17	0	1.58	0.17	0.75	2.67	0.17	1.83	2.33
Whatarangi	2.65	0.88	0.06	2.12	0.06	4.82	5.71	0.06	0.29	1.00	0.35	0.06	1.76	0.35	3.53	4.76

The GLMM testing the effects of fragmentation parameters on the number of birds detected per count was performed on each bird species or group of species listed in Table 2.6 (see Table 2.8 for results). The example below shows a typical summary output of the model using response variable y = number of bellbird per count (Table 2.7).

Table 2.7: Summary output of the GLMM testing the effect of altitude, area, ADRA, and dH, on the number of bellbird detected per 5-min count in 18 lowland forest sites on Banks Peninsula at 142 fixed stations, taking into account the random effects of the year of the count and the location of count stations within sites. Bold p-values indicate a significant effect ($p < 0.05$).

Generalized linear mixed model fit by maximum likelihood

Family	Poisson (log)				
Formula	*Bellbird ~ Alt + log(Area) + log(ADRA) + log(dH) + (1 | as.factor(Year)) + (1 | Site/Block)*				
Information	AIC	BIC	logLik	deviance	df. residuals
criteria	1778.4	1812.5	-881.2	1762.4	519
Scaled residuals	Min	1Q	Median	3Q	Max
	-1.8749	-0.5203	0.0109	0.4187	3.4396
Random effects	Groups	Name	Variance	Std. Dev.	Number of obs.
	Block:Site	(Intercept)	0.01792	0.1339	37
	Site	(Intercept)	0.07307	0.2703	18
	as.factor(Year)	(Intercept)	0.04103	0.2026	8
					527
Fixed effects		Estimate	Std. Error	z value	p(>|z|)
	(Intercept)	1.56012	0.33570	4.647	< 0.001
	Alt	-0.55843	0.37333	-1.496	0.13470
	log(Area)	-0.19688	0.10721	-1.837	0.06628
	log(ADRA)	0.04299	0.05858	0.734	0.46297
	log(dH)	0.36522	0.11976	3.050	**0.00229**
Correlation of		(Intercept)	Alt	log(Area)	log(ADRA)
Fixed Effects	Alt	-0.357			
	log(Area)	-0.816	-0.118		
	log(ADRA)	0.350	-0.204	-0.187	
	log(dH)	0.415	-0.175	-0.443	-0.352

All bird species and group of species analysed in the GLMM responded differently to each fragmentation parameter (Table 2.8). In total, 17 significant effects ($p < 0.05$) were found by the models, i.e. 28.3 % of all the bird-parameter pairs tested in this analysis: more than would be expected by chance only (5 %).

Table 2.8: Coefficients and p-values (in brackets) from summary outputs of generalized linear mixed models testing the effects of fragmentation parameters on the number of birds detected per 5-min count in 18 lowland forest fragments on Banks Peninsula (data 2005-2016). Bold p-values indicate a significant effect ($p < 0.05$), highlighted in green when positive, in red when negative.

Response var.	Altitude	log(Area)	log(ADRA)	log(dH)
Bellbird	-0.558 (0.135)	-0.197 (0.066)	0.043 (0.463)	**0.365 (0.002)**
Blackbird	-0.221 (0.593)	-0.078 (0.511)	0.090 (0.165)	-0.045 (0.735)
Kereru	**-1.649 (0.048)**	-0.473 (0.052)	**0.281 (0.026)**	0.351 (0.185)
Silvereye	0.107 (0.913)	-0.291 (0.252)	-0.213 (0.116)	**0.612 (0.032)**
Pollinators	-0.097 (0.792)	**-0.235 (0.028)**	-0.055 (0.341)	**0.389 (< 0.001)**
Dispersers	-0.194 (0.536)	**-0.226 (0.015)**	-0.017 (0.738)	**0.313 (0.002)**
Fantail	-1.033 (0.070)	**0.410 (0.044)**	-0.104 (0.202)	-0.293 (0.105)
Brown Creeper	**2.041 (0.040)**	0.23 (0.384)	-0.170 (0.235)	0.202 (0.480)
Grey Warbler	-0.244 (0.729)	-0.222 (0.281)	-0.093 (0.430)	0.464 (0.054)
Tomtit	**2.723 (0.036)**	-0.198 (0.595)	**0.600 (0.010)**	0.042 (0.926)
Rifleman	**2.810 (< 0.001)**	-0.291 (0.106)	**0.424 (< 0.001)**	0.389 (0.113)
Non-mut. native	0.249 (0.408)	0.043 (0.622)	-0.021 (0.624)	0.089 (0.328)
Song Thrush	**-0.796 (0.022)**	-0.162 (0.136)	**0.288 (< 0.001)**	-0.183 (0.103)
Finches	-0.337 (0.321)	0.079 (0.430)	0.084 (0.102)	-0.188 (0.066)
Non-mut. exotic	**-0.584 (0.047)**	0.013 (0.878)	0.071 (0.109)	-0.119 (0.177)

Altitude was negatively related with the detection of kereru (Figure 2.3c), song thrush, and the overall community of non-mutualist exotic birds, but positively related with the number of brown creepers, tomtits and riflemen (Figure 2.3b). Increasing area had no significant effect on any individual bird species apart from a slight increase in fantail detection numbers, but was negatively related with the guild of mutualist birds (pollinators and dispersers). Connectivity index ADRA, which is specific to each site and its immediate neighbourhood, had a positive effect on kereru, tomtit (Figure 2.3d), rifleman and song thrush, whereas dH, a connectivity index based on the importance of each site in the overall landscape connectivity, was positively related with the detection of bellbird (Figure 2.3a), silvereye, and the community of all mutualist birds (Table 2.8).

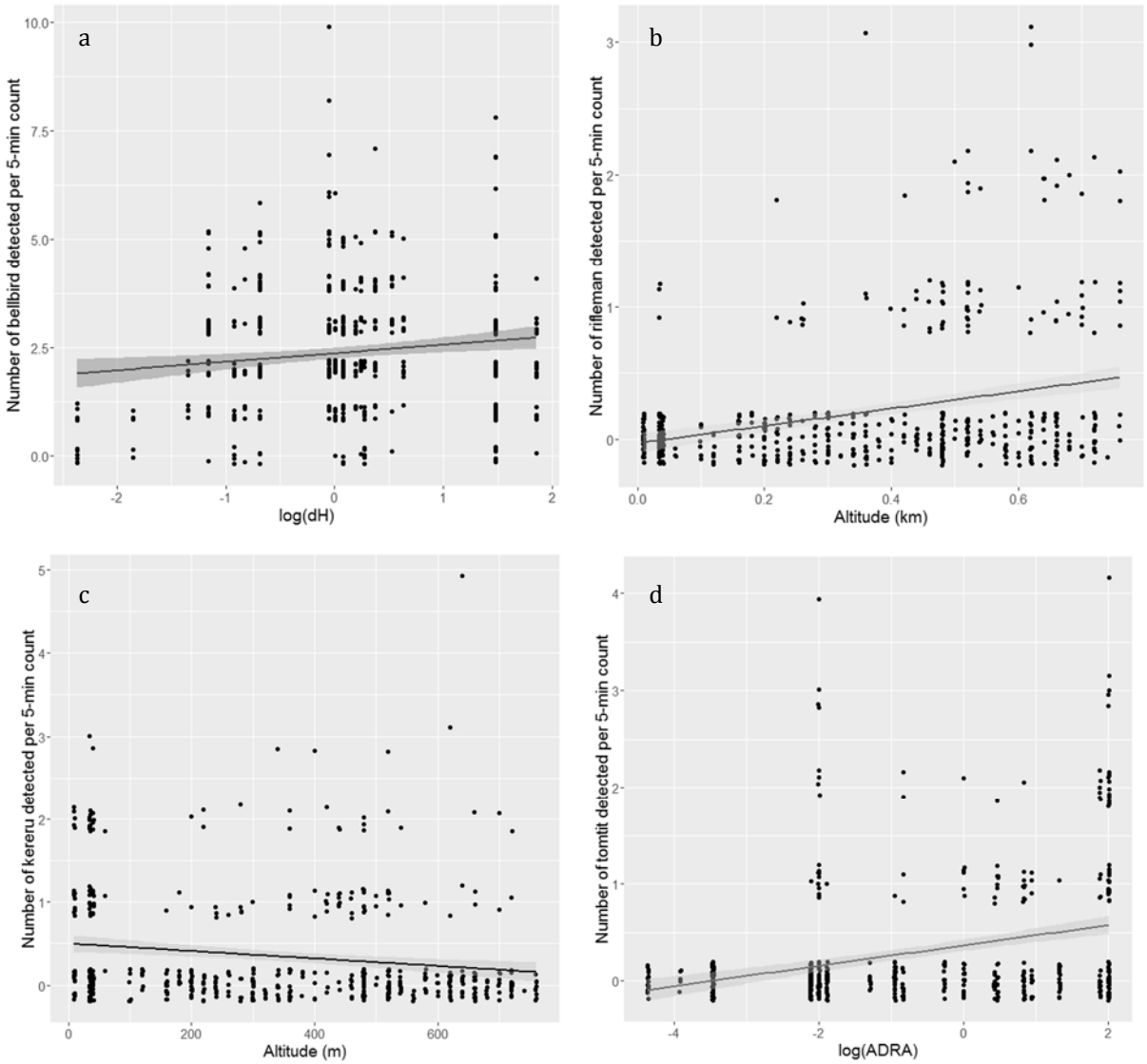

Figure 2.3: Scatter plots (jittered) with fitted regression lines indicating the significant effect ($p < 0.05$) of altitude and connectivity indices dH and ADRA on the abundance of four native bird species detected per 5-min count in 18 lowland forest fragments on Banks Peninsula (data 2005-16): (a) bellbird against log(dH), (b) rifleman against altitude, (c) kereru against altitude, and (d) tomtit against log(ADRA).

IV. Discussion

Limitations and advantages of 5-min bird counts

Similarly to most bird count methods, the accuracy of 5-min bird counts depends heavily on environmental conditions. Weather-induced (e.g. wind, rain) and site-specific noises (e.g. stream water sounds, cicada songs), as well as vegetation structure, are all factors affecting the chance of bird detection, because of their influence on both the behaviour of birds present in a site and on the observers' ability to detect them (Dawson & Bull 1975). When bird counts are carried out by various observers, their capacities to identify and quantify birds can differ between individuals and evolve over time. Moreover, birds' activity and detectability vary hourly and seasonally (Dawson & Bull 1975; Hartley 2012).

Another variation in bird detectability concerns species-specific conspicuousness. For example, exotic finches and other open-land birds are very vocal, and can be difficult to tell apart between species, whereas native forest birds have more distinctly recognizable but less frequent calls that can easily occur outside of the duration of the counts. On Banks Peninsula, tui are present as a small population (72 birds translocated in 2009-10, and probably about 100-150 birds currently present: Laura Molles, Lincoln University, pers. comm.), and although there has since been many reports of tui sights around inhabited areas, their detection in native forest remnants is still rare, possibly as a result of their attraction to highly-rewarding food sources in planted gardens. A few native birds tend to remain mostly silent in the presence of an observer (e.g. tomtit, kereru) and are often detected by sight rather than acoustically. In some cases, an increase in conspicuousness can be attributable to more vigorous calls by individuals looking for a mate after a significant population decline (Hartley 2012). Some birds often travel in small groups (e.g. most finches, silvereye, and to a smaller extent brown creeper and rifleman), so they are usually counted either as absent or as present in more than one individuals. The number of birds present in larger flocks is difficult to estimate, and the independence between individuals cannot be assumed (Hartley 2012). Highly mobile birds are difficult to quantify with certainty, because two separate calls from a bird species heard from two different directions within a substantial time interval could have been emitted either by a single bird that moved, or by two distinct individuals. Finally, some observers are unable to hear the high frequency of the rifleman's call, which includes a range of ultrasounds (Krull et al. 2009; Mortimer 2013).

Given the high variability in birds detectability between sites, times, and observers, it is important to recognize that 5-min bird counts are not a precise density measure but rather a detection index (Hartley 2012). A single count cannot be considered representative of the local

bird community, but repeated counts over time at various locations within a site allow for a better estimation of local bird densities. The popularity of the 5-min bird count method in New Zealand has allowed for the creation of a 5MBC database of over 120,000 counts carried out since the early 1970s, managed and regularly updated by ECan with additional data (Hartley 2012). This database can be accessed to compare former local data with new counts carried out at similar locations, which has allowed for the inclusion of 2005-12 data in the present study.

A few studies have shown that long-term trends in the number of birds detected per 5-min count were directly related to real decline or increase in population sizes (e.g. Murphy & Kelly 2001; Elliott et al. 2010). However, in the absence of a significant linear trend, changes in bird numbers do not necessarily reflect actual fluctuations in bird populations; slight local variations between bird numbers across time should rather be considered an artefact of transitory changes in bird detectability (Hartley 2012). In the present study, the absence of linear change in bird numbers across multiple counts repeated between 2005 and 2016 in 18 sites on Banks Peninsula is a good indicator of the relative stability of local bird populations. The average number of birds detected per count over the past decade in a particular site is more likely to reflect the relative bird density at this site in any given year within this decade than a restricted number of local counts during that year. For this reason, the average number of mutualist birds detected per count in each study site between 2005 and 2016 is used in the next chapters, where I assess the effects of bird densities and fragmentation parameters on pollination, seed dispersal, and inbreeding depression of *Fuchsia excorticata*.

Effect of fragmentation parameters on exotic bird densities

The most common exotic birds detected in the 18 study sites during 5-min bird counts were the blackbird, song thrush, and various finches. The analyses found no significant effect of fragmentation parameters on the detection of blackbird, finches, and the overall exotic bird community, but there was a higher number of song thrushes in sites with higher site-scale connectivity (ADRA). Barbaro et al. (2012) found that both *Turdus* species, blackbird and song thrush, were present in abundance at the edge and interior of native forests. Most finches were not detected at the core of forest fragments but frequently present at the edge, where they breed and roost, and where additional food sources complement their mostly open-habitat foraging (Barbaro et al. 2012). As generalist species, exotic birds are able to adapt to various vegetation types and landscape configurations, so it is not surprising that their presence was not significantly affected by forest connectivity or patch area, which was also highly correlated with Shape Index in this study. Increasing altitude however was negatively related to the overall

abundance of exotic birds in general, and of the song thrush in particular, which is consistent with the altitudinal range of introduced land bird species. An implication of their widespread distribution, including in native forest patches, is that they may become notable competitors to some native forest birds, especially during winter months when resources are limited and mutualist birds experience a shift in their diet from feeding on nectar and fruits to mostly invertebrate consumption (O'Donnell & Dilks 1994).

Fewer native mutualist birds in large forest fragments

Apart from the slightly positive effect on fantails, area had no significant effect on any bird species. Most of the coefficients generated by the GLMMs for area were negative on native birds, resulting in a significantly negative effect of area on all pollinator and disperser birds. This result is conflicting with the general assumption that larger native habitats are beneficial to endemic bird diversity, as demonstrated in several studies. For example Sekercioglu et al. (2002) found that native insectivorous bird communities were poorer in small fragments of about 5 ha than in larger forest patches of over 200 ha. Flocking birds had higher absence rates in patches smaller than 10 ha than in larger forest fragments (Stouffer & Bierregaard 1995). For the conservation of tropical forest birds, Sodhi et al. (2004) insist on the importance of including sufficient forested area in protected reserves, because small fragments are more likely to lack adequate resources, to enable parasitism and species invasion, and to contain populations not abundant enough to resist environmental stochasticity. Overall, most studies agree that bird population sizes in fragmented forests depend on their dispersal ability, with small ground-nesting insectivorous birds and canopy frugivores being more at risk of disappearing from small forest patches than highly mobile honeyeaters that are commonly feeding at forest edges and in forest gaps (Sodhi et al. 2004). In my study, the overall negative effect of area on mutualist birds was thus unexpected. Although repeated counts over the past decade have confirmed the generally low numbers of native birds, especially mutualist birds, in large forest patches, it is possible that these numbers were underestimated because of the inherent difficulty to detect birds where the woody vegetation is dense and widespread. However, it is still clear from the analyses that significant increases in area (sometimes by over a tenfold) between sites do not result in proportional increases in native bird populations, as might have been predicted. If this trend reflects an actual low density of native birds in large reserves, a potential explanation could be the recent history of deforestation and regeneration on Banks Peninsula: it is possible that some of the forest fragments that are large today still have important areas in the early stages of forest regeneration, with little understory and poor conditions for native birds. Large

patches with extended areas of dense forest cover may also be difficult to control for introduced predators, especially rats, which in high numbers may be preventing the breeding success of native bird populations. Banks Peninsula is scattered with many forest fragments left with relatively high connectivity levels compared to other highly deforested regions of New Zealand, hence the difficulty to prevent local recolonization by small invasive mammals. Current bird populations in Banks Peninsula forests are thus depleted of species requiring larger forested areas (e.g. kaka, kokako), and of species which cannot cope with current pest densities (e.g. saddleback, kakariki).

Importance of connectivity for native forest birds

In this study I tested two measures of forest connectivity: ADRA was a site-scale index calculated using the area of, and distance to directly surrounding forest patches (within 500 m), whereas dH reflected the importance of each site in the overall landscape connectivity (Harary index) based on distances between patches. ADRA was positively correlated with kereru, tomtit, and rifleman numbers, whereas dH had a significant positive effect on bellbird, silvereye, and the guild of mutualist birds. Tomtit and rifleman are small insectivorous birds with life-history traits associated with high sensitivity to forest fragmentation, such as low dispersal abilities and vulnerable nesting habits (Sodhi et al. 2004). The influence of ADRA on their distribution shows that their populations can be favoured by increasing the number and reducing the distance of forested patches around their original habitat. Despite the kereru's ability to travel over long distances between suitable habitats, the positive effect of ADRA on kereru abundance may be related to a preference towards well-aggregated clusters of habitat fragments, where they can spend less time and energy moving between patches. Bellbird and silvereye, on the other hand, are highly mobile species that are commonly seen in non-forested habitats. In their study of avian assemblages in fragmented forests of Banks Peninsula, Barbaro et al. (2012) found that two thirds of all observations of silvereye and 42% of all observations of bellbirds were made at forest edges, as opposed to observations in forest interiors. Their increase in density at sites with higher dH values indicates that these mutualist birds tend to build movement decisions based on their perception of the whole landscape connectivity, rather than on their immediate surroundings only. Thus, small forest fragments are less likely to be depleted of mutualist birds when belonging to a well-connected network of native forest patches than when isolated.

V. Conclusion

Using a large dataset of 5-min bird counts carried out between 2005 and 2016 in 18 native forest fragments on Banks Peninsula, I found that bird communities were generally stable over time, with no evidence of linear increase or decline in any particular species across the study period. Among the various measures used to test the effects of forest fragmentation on bird densities, area surprisingly had no positive influence on the number of birds detected per count. Large areas were instead associated with lower counts of native mutualist birds. The other main component of habitat fragmentation, patch connectivity, was tested at the site and the landscape scale. Small insectivorous native birds and a large native frugivore bird were positively correlated with patch-scale connectivity, whereas a highly mobile native honeyeater and a flocking generalist were both detected in higher abundances at sites with higher importance for the overall landscape connectivity. Altitude is not a fragmentation parameter but is known to affect the distribution of most bird species in New Zealand. In this study, as altitude increased, small native forest birds were generally more abundant, while the community of all exotic birds was detected in smaller numbers.

The main finding of this chapter – that for the surviving native birds, patch connectivity mattered more than area – has important implications for the conservation of native avifauna. First, more research is needed to determine the reason of the lack of a positive effect of area on native birds, so that the current situation may be improved in the future. Large reserves may have higher densities of invasive mammal predators, keeping local breeding success of native birds at a low level. Another hypothesis is that the ongoing regeneration of native forest following conservation efforts may have allowed for habitat expansion at a faster pace than the local bird populations, which may be slow to recolonize those relatively new forested areas. Second, the importance of connectivity for all types of native forest birds implies that even small patches of native forest are worth protecting and managing for adequate resources and minimal threats. Allowing for the establishment of small regenerating forest stands will improve the connectivity level of the small network of neighbouring patches, as well as the overall landscape connectivity, thus facilitating the sustainability of higher numbers of native forest birds. Finally, despite the high dispersal ability of native mutualist birds, which are capable of travelling long distances between forested habitats, isolated fragments may be overlooked by foraging pollinators and seed dispersers. A possible long-term consequence of low visitation by mutualist birds is the lack of pollen immigration and gene flow into isolated patches, with an increased likelihood of inbreeding depression for plants that rely on birds for reproduction. Those hypotheses are tested in the following chapters.

CHAPTER 3:

Lowland forest fragmentation and pollination service of *Fuchsia excorticata* on Banks Peninsula

The female Fuchsia excorticata flower, recognizable by its non-functional anthers, has a green corolla during its young, receptive phase. A small amount of blue pollen has been deposited on the surface of its yellow stigma. (Photo Marine Aubert)

I. Introduction

In New Zealand, the earlier assumption that pollination systems of the native flora were dominated by generalist insects, and that birds were unimportant contributors (Godley 1979; Lloyd 1985; Clout & Hay 1989), has been revised and contradicted by recent advances in the field of pollination ecology: for native plants with multi-seeded fruits, birds have demonstrated better pollination efficiency than insects, contributing to higher fruit and seed sets than insect pollination (Anderson 2003; Kelly et al. 2010; Pattemore & Wilcove 2012; Anderson et al. 2016). Although insect visitations to otherwise bird-visited native flowers are frequent, they often remain insufficient to sustain the essential cross-pollination of these species (Pattemore & Wilcove 2012; Pattemore 2013). Among 85 New Zealand plant species with recorded observations of bird-visited flowers, pollination by bird appears to be important for the reproduction of 48 species (Kelly et al. 2010). On offshore pest-free sanctuaries with high bird densities, inter- and intra-specific competition between honeyeaters ensures the visitation of a wide range of food sources with high flower visitation rates, which is not observed in bird-deficient mainland sites (Anderson 2003). Five endemic bird species possess brush tongues that are well adapted to feed on nectar, and have been identified as former important pollinators: stichbird, kaka, and kokako are now severely range-reduced, whereas tui and bellbird still remain present throughout the country, but in lower abundances and smaller ranges than during pre-human times (Holdaway 1999; Anderson et al. 2006; Kelly et al. 2006; Kelly et al. 2010). Because of the prevalence of nectar in their diet, and their ability to cross-pollinate efficiently a large number of native flowering species, bellbird and tui are currently amongst the most proficient pollinator birds of New Zealand plants (Craig et al. 1981; Anderson 2003; Anderson et al. 2006; Kelly et al. 2006). Silvereye is a recently established, naturalized and considered native widespread generalist that also contributes to the pollination of many native plants, however its frequent nectar-robbing behaviour on large flowers is limiting the extent of its contribution to pollination service in some species (Delph & Lively 1985; Kelly et al. 2006; Robertson et al. 2008). In contrast, introduced birds rarely visit native flowers (5% of all visits to 18 plant species in Kelly et al. 2006), and similarly to silvereye the exotic short-beaked flower visitors such as chaffinch and sparrow are technically unable to achieve efficient cross-pollination on native flowers with long tubular corollas (Kelly et al. 2006).

As a result of New Zealand's forest cover loss of over 77% since pre-human times, combined with the considerable ongoing impact of predation by introduced mammals nationwide, the native avifauna has suffered a large decline in density and diversity (Holdaway 1989; Holdaway 1999; Tennyson 2010). The reduction in richness, abundance and composition

of the pollinator guild has been linked with increasing evidence of disruptions in plant-pollinator interactions, with negative effects on the regeneration of native plants (Kaiser-Bunbury et al. 2010; Kelly et al. 2006; Iles & Kelly 2014). At North Island sites where bellbird and stitchbird are lacking, Anderson et al. (2011) found that the New Zealand shrub *Rhabdothamnus solandri* was severely pollen-limited, with seed-set reduced by 84% and juveniles 55% less abundant than on offshore bird sanctuaries. Similarly, *Alseuosmya macrophylla*, another native shrub pollinated by birds, was highly seed-limited on the mainland in comparison to offshore sites in a bird sanctuary where both bellbird and stitchbird were abundant (Pattemore & Anderson 2013). In a study assessing the pollination of seven New Zealand bird-pollinated plants, Kelly et al. (2010) found that only one species was getting sufficient pollination service at all sample sites, the others producing low seed-set where visitations by birds were limited. The self-compatible *Alepis flavida*, and hermaphrodite *Fuchsia excorticata*, were producing adequate fruit set, most likely because of their ability to self-pollinate even in the absence of flower visitors (Anderson et al. 2006; Robertson et al. 2008).

Following habitat loss, local extinction rates in remaining fragments are much faster for animals than for plants, which are capable of holding important extinction debts (Kuussaari et al. 2009; Kaiser-Bunbury et al. 2010). The long-term persistence of many plant species is dependent on the perpetuation of the mutualistic interactions in which they are involved (Bond 1994; Sekercioglu et al. 2004). Where mutualistic interactions between plants and birds are reduced by the lack of mutualist birds, plant species that rely on birds for reproduction are facing regeneration failure through a general reduction in seed-set and seed fitness (Kaiser-Bunbury et al. 2010). In fragmented landscapes, small isolated forest fragments are the most likely to suffer decreased mutualistic interactions between plants and pollinators, resulting in inadequate pollen transfer and low seed sets, whereas large plant populations are expected to attract more pollinators, experience higher visitation rates and pollination success (Mustajarvi et al. 2001). Rates of self-pollination and mating between close relatives are also higher in small, isolated populations, which could lead to high levels of inbreeding depression with reduced fitness within the next generations (Mustajarvi et al. 2001).

In addition to population size, plant population density is known to affect visitation rates and foraging behaviours of flower visitors. Sparse plant populations have been linked with low visitation rates and increased within-plant pollen transfers (Mustajarvi et al. 2001; Wilcock & Neiland 2002). Although various studies have found that pollinator abundance and diversity tend to increase with patch area, plant reproductive success wasn't always correlated with plant population size. For example, for a bumblebee-pollinated herb with a distinct patchy distribution in Finland, pollination rates were higher in small grassland fragments and sparse

populations, however the lower visitation rates in large patches with dense populations were more likely to result in cross-pollination (Mustajarvi et al. 2001). Where bird-pollinated plant populations occur at low densities and their mutualist birds are present in low abundance, dioecious plants are at particular risk of pollination failure because they absolutely require pollen transfer between individuals of the two sexes (Wilcock & Neiland 2002). The reduction in abundance and diversity of mutualist birds associated with forest fragmentation affects competition between and within species, leading to modifications in foraging behaviours and food preferences, including a decrease in the degree of generalization of pollinator species (Fontaine et al. 2008). At low bird densities, such modifications in pollinator diet may threaten the persistence of plant species that have restricted distribution, or offer lower energetic rewards to birds (Jordano 1987). Ultimately, pollinator declines in fragmented habitats are not only affecting single plant-pollinator interactions, but have a significant impact on entire pollination networks (Wilcock & Neiland 2002). The loss of a mutualist species in forest fragments can thus be associated with cascading local extinctions (Rathcke & Jules 1993; Wilcock & Neiland 2002). Overall, isolated fragments are thought to be at high risk of pollination failure and pollen limitation, because of the reduced density and diversity of pollinators, and the resulting modifications in their foraging behaviours, including a reduction in flower visitation rates, a decrease in average pollen loads per visit, and inconsistency in pollen transport between sexes (Wilcock & Neiland 2002). Local increases in pollinator densities resulting from predator control have proven effective in restoring adequate pollination service for some species (e.g. Robertson et al. 2008; Bell 2010; Iles & Kelly 2014), but not for others (Kelly et al. 2005). However when mutualism failure has led to local losses in genetic diversity, sustainable genetic structure cannot be regained through the restoration of pollination mutualism only: strategic translocations or immigrations are necessary to reintroduce lost genotypes in the population. Severely inbred populations may be slow to recover, and bottlenecked populations may fail to survive stochastic events despite the reinstatement of seemingly adequate cross-pollination (Innes et al. 2010).

Fuchsia excorticata is a bird-pollinated gynodioecious native forest tree that has female and hermaphrodite individuals (Godley 1955). Hermaphrodite flowers are larger and produce significantly more nectar than female flowers (Delph & Lively 1985). Its three main flower visitors are bellbird, tui and silvereye, which all visit *F. excorticata* flowers preferentially during their early phase, and tend to ignore the practically nectarless older flowers (Delph & Lively 1985). Bellbird and tui provide legitimate pollination service by inserting their bill in the tubular corolla while collecting pollen (from hermaphrodite flowers) on their forehead and depositing it onto the yellow stigma of flowers of both sexes (Delph & Lively 1985). Silvereyes

similarly approach the small female flowers from the front, but their beaks are too short to reach the nectar of larger hermaphrodite flowers, so they rob these larger flowers by perforating the side of the tubular corollas. This behaviour prevents the collection and potential transmission of hermaphrodite pollen to other flowers (female or hermaphrodite), so the contribution of silvereye to *F. excorticata* pollination is negligible (Godley 1955; Delph & Lively 1985). Hermaphrodite *F. excorticata* flowers are able to self-pollinate, whereas females are pollinated only through external input of pollen from hermaphrodite flowers. Previous studies on *F. excorticata* pollination have shown that pollen scores on hermaphrodites are usually high, but on females fluctuate considerably between sites (Robertson et al. 2008; Iles & Kelly 2014). For hermaphrodites, the seeds produced via self-pollination suffer high inbreeding depression (Robertson et al. 2011). Pollination failure in female *F. excorticata* flowers has been linked to low pollinator densities at sites with no predator control, where female trees were highly pollen- and seed-limited (Robertson et al. 2008; Iles & Kelly 2014). *Fuchsia excorticata* density also affects flower visitation rates, with isolated trees receiving fewer visits by pollinators than trees within dense populations, even at sites with high pollinator densities (Bell 2010). Adequate pollination service to females, and effective cross-pollination between individuals of both sexes, only occur when pollinator densities are high enough to allow for sufficient visitation rates throughout the population. Where several pollinator species coexist, the large and dominant tui tend to defend flowering trees against the smaller bellbird and stitchbird, which spend less time feeding on each tree before being chased away, hence being more likely to achieve cross-pollination (Anderson 2003; Anderson et al. 2016). In isolated forest fragments, where pollinator diversity and density are reduced, flower visitors are expected to adapt their foraging behaviours for optimal energy intake, possibly ignoring the less rewarding female flowers and reducing their movements between trees (Craig et al. 1981; Anderson 2003).

In the previous chapter, I showed that the guild of *F. excorticata* flower visitors (bellbird, silvereye and tui) was significantly more abundant in well-connected forest fragments, but their densities did not increase with area. In this chapter, I aimed to identify which fragmentation parameters were accurate predictors of *Fuchsia excorticata* pollination. Are the factors influencing pollination the same that affect mutualist bird distribution? What bird densities are required for sufficient pollination service?

II. Methods

Pollination service

I estimated local pollination service using the visual pollen load measure described by Robertson et al. (2008) to assess pollination success on *F. excorticata*. In their study, the visual score of blue pollen present on the surface of the stigma was well correlated with fruit set, and with honeyeater visitations rates on female trees. Pollen loads are usually high on hermaphrodite flowers because of their ability to self-pollinate (Robertson et al. 2008; Iles & Kelly 2014). In contrast, low pollen loads often seen on females are an indication of local pollination failure. I scored the pollen load on receptive flowers as the percentage (visual estimate) of visible blue pollen present on the surface of the yellow stigma: (0) 0%; (1) 1–5%; (2) 6–20%; (3) 21–40%; and (4) 41–100%, using the methodology developed by the University of Canterbury and Landcare Research for the National Pollination Survey (Robertson et al. 2008). Based on the relationship shown between pollen load and fruit set, a local average pollen load index above 1.5 is an indicator of sufficient pollination service (Robertson et al. 2008).

Pollen load scores (PLS) on *Fuchsia excorticata* flowers were recorded at seven sites during spring 2013 and at eleven sites during spring 2014. Up to 15 trees were sampled in each site (less in sites where the total flowering *Fuchsia* population was smaller), including up to 6 females per site (Table 3.1). Hermaphrodite trees (whose offspring are only hermaphrodites too) always outnumber female individuals, which produce offspring of both sexes in equal proportions, hence *F. excorticata* populations almost never have a female/hermaphrodite ratio exceeding 33 %. As a result, female trees can be difficult to find in some sites, especially in populations where trees are sparsely scattered within dense mixed vegetation. On each tree, I scored the pollen load on 10 receptive flowers in their early to medium stage (as indicated by a green corolla), randomly selected across several branches (3 trees had 9 flowers sampled, and 3 others had respectively 11, 7 and 6 flowers scored for pollen load).

I tried to sample the same trees in sites where pollen loads were measured both years, but most of the trees used during the first sampling season were either not found again (tag missing), or tree had died, or it had too few accessible flowers to score pollen loads on the second sampling year. Out of the 164 trees sampled across the two seasons, only 14 were replicated both years (8.5 % of all trees), including 4 females and 10 hermaphrodites; the 150 other trees were each sampled once.

Table 3.1: Number (n) of female (F) and hermaphrodite (H) flowering *Fuchsia excorticata* trees measured for pollen load scores (PLS) during springs 2013 and 2014, and local average PLS per tree, in 13 lowland forest sites on Banks Peninsula.

	2013				2014			
	F		**H**		**F**		**H**	
Site	**n**	**PLS**	**n**	**PLS**	**n**	**PLS**	**n**	**PLS**
Cloud Farm	5	1.64	10	2.59	3	1.64	3	3.29
Hay	0		0		2	3.10	1	2.30
Hinewai	5	0.70	10	2.41	0		0	
Magnet Bay	0		0		5	0.84	9	2.09
Montgomery	3	0.80	9	2.50	5	2.15	5	2.85
Mt Pearce	0		0		3	2.27	7	2.96
Mt Sinclair	0		4	2.10	3	0.67	4	1.70
Oashore	0		0		1	3.80	7	2.78
Otepatotu	5	2.22	10	1.99	3	1.90	5	3.04
Tipperary Gully	0		0		1	1.90	4	2.87
Tutakakahikura	0		0		5	1.98	6	1.73
Waghorn	3	1.53	5	2.08	0		0	
Whatarangi	6	1.38	9	2.40	6	0.97	6	2.63
Total	27		57		37		57	

Site-specific parameters: biotic and abiotic factors

The successful pollination of *F. excorticata* flowers is directly related to their visitation by efficient pollinators. On Banks Peninsula, *F. excorticata*'s main pollinator is the bellbird, and its direct competitor is the silvereye which feeds on nectar usually without achieving pollination. Both birds are affected in various ways by forest fragmentation: in Chapter 2 I found that the guild of flower visitors (bellbird, silvereye, and tui) was detected in significantly higher numbers at sites with high connectivity levels (landscape-scale connectivity index dH), and in lower densities within large sites. Site-scale connectivity index ADRA had no effect on flower visitors, but could have an influence on honeyeaters' feeding behaviour, so ADRA was also included in the assessment of pollination service. The altitudinal range of bird distribution varies between species, with both bellbird and silvereye decreasing in density with increasing altitude.

The foraging behaviours of bellbird and silvereye may be affected by local vegetation structure, including edge effects and local *F. excorticata* densities. In this study, I used a numerical scale of 0 to 2 to describe the edge aspect of the immediate vegetation surrounding flowering *F. excorticata* trees: (0) for trees located under closed forest canopy, (1) along forest tracks, and (2) at the actual edge of the forest fragment, along the boundary between native

forest and open land. As no standard measurement of *F. excorticata* density was originally included in the experiment design, I used a subjective population density scale of 1 to 3 based on personal field observations, which estimates visually the proportion of *F. excorticata* in the overall canopy cover of each site within the area where pollen scores were measured: (1) low *F. excorticata* density with less than 10% of the canopy cover, (2) medium density with 10-40% of the canopy cover, and (3) dominant species making over 40% of the canopy cover.

The tui is an important nectar-feeder and efficient pollinator of *F. excorticata* flowers, however its density on Banks Peninsula is so low that its effect on *F. excorticata*'s pollination could not be estimated in this study. Bellbird was the main visitor to *F. excorticata* flowers in the study area, so its presence in high densities was expected to affect positively their pollen loads. As the silvereye visits *F. excorticata* flowers without achieving cross-pollination, its presence in high abundance was expected to have either no effect or a negative influence on *F. excorticata*'s pollination service. I used the average number of bellbirds and silvereyes per count as presented in Table 2.5, calculated from the 2005-16 dataset of local bird counts.

For each study site where pollen loads were measured, altitude, area, dH, relative *Fuchsia excorticata* density, and nectarivorous bird densities are presented in Table 3.2.

Table 3.2: Altitude, area, dH value, importance of *F. excorticata* in the forest canopy, and average number of flower visitors (bellbird and silvereye) detected per 5-min count (data 2005-16) at 13 study sites on Banks Peninsula.

Site	Alt. (m)	Area (ha)	dH (%)	ADRA ($ha.m^{-1}$)	*F. exc.* density	Bellbird	Silvereye
Cloud Farm	620	4.05	1.88	1.60	3	2.65	2.65
Hay	35	6.37	0.95	0.12	1	3.32	1.21
Hinewai	400	93.44	4.39	7.48	3	2.31	0.88
Magnet Bay	240	29.49	1.21	0.77	2	0.94	1.12
Montgomery	500	23.38	0.50	0.13	3	2.83	2.29
Mt Pearce	540	38.07	1.32	3.77	3	0.88	0.47
Mt Sinclair	740	74.72	6.40	1.01	2	2.08	2.46
Oashore	240	12.87	1.08	0.03	1	2.53	2.56
Otepatotu	660	16.84	1.00	2.30	3	1.81	0.75
Tipperary Gully	300	2.84	0.09	0.01	1	0.35	2.41
Tutakakahikura	380	12.89	0.44	2.57	2	2.09	1.91
Waghorn	680	8.60	1.69	1.53	2	3.25	0.58
Whatarangi	580	5.22	1.27	0.43	3	2.65	2.12

Statistical analyses

All statistical analyses were performed using the program R version 3.1.1 (R Core Team 2014). The average pollen load score per *F. excorticata* tree was calculated for the 164 trees using a total of 1771 visual pollen scores, separately for the two sampling seasons. The average pollen load was calculated for each tree in each year. Plant mean pollen load scores were normally distributed. As five sites had been sampled both years (Table 3.1), I used an ANOVA (*aov* command in R) to test whether sampling year had an effect on the average pollen load score (PLS) per tree in these sites (Table 3.3). I used the formula: *aov(formula = PLS ~ Site * Year)*.

Table 3.3: Analysis of variance table from the ANOVA assessing the effect of site and sampling year on the average pollen load score (PLS) per *Fuchsia excorticata* tree. Bold p-values indicate a significant effect ($p < 0.05$).

Response variable	Parameter	Df	Sum Sq.	Mean Sq.	F value	p(>F)
PLS	Site	4	6.45	1.6119	2.523	**0.0461**
	Year	1	0.27	0.2742	0.429	0.5140
	Site : Year	4	4.50	1.1240	1.759	0.1437
	Residuals	94	60.06	0.6390		

From the dataset of mean pollen load per tree recorded in the same sites during two sampling seasons (104 trees in 5 sites), the effect of site on the average pollen score per tree was significant, not the effect of year across all sites, nor the effect of year within each site (Table 3.3). This indicates that between sites sampled twice, the average PLS per tree varied significantly between sites, but not within sites between years: site-specific pollination scores were apparently consistent throughout the years. Therefore, sampling year was not taken into account in the following analyses. I tried allowing for data structure by either including a random term for tree ID in the model, or by averaging pollen load scores per tree across both years for the 14 trees sampled in both years, but their proportion was so low that both methods didn't affect the analysis outcome, so I used the total of 178 average PLS per tree per year to analyse in the model.

Similarly to previous studies, pollen load scores on *F. excorticata* trees were significantly different between females and hermaphrodites, therefore the following analyses were performed separately for each sex.

To test the parameters affecting *F. excorticata* pollination success, I used the raw dataset of 1771 visual pollen scores to run, separately for each sex, generalized linear mixed models (GLMM) with Poisson error distribution (lme4 package in R), allowing for data structure by

including a random term for tree within site, and analysed with an ANOVA based on Chi-squared test (Anova command from car package in R). Because I had eight predictors, most of which varied at the level of site (with n = 13 sites for the pollination data), I used some preliminary analysis to select the 3-5 best predictors for testing.

Initially I ran each predictor separately in its own GLMM, and then I used the significance tests and AIC values from those GLMMs to rank the predictors and select the top predictors for further testing. Predictors were selected if they were significant or nearly so ($P < 0.10$) or had AIC values close to the best single model.

I used the formula: glmer(formula = PLS ~ x + (1|Site/TreeID), family = "poisson"), where the explanatory variable x was respectively altitude, area, connectivity indices dH and ADRA, edge, subjective measure of F. excorticata density, mean number of bellbird, and mean number of silvereye detected per count. Area, dH and ADRA were log-transformed in order to increase the normality of their distribution across data.

Parameters with an individual effect significant at $p < 0.1$, or an AIC near to the best single predictor, were then included in a model selection process, starting with a new GLMM with Poisson error distribution and a random term for tree within site, then manually removing fixed-effect parameters one at a time (drop1 command in R, with test = « Chisq »). This stepwise backward model selection was repeated until no parameter elimination would decrease further the model's AIC. The final model best explaining the data was then analyzed with an ANOVA based on Chi-squared test.

III. Results

Pollination scores on hermaphrodite *F. excorticata* flowers were always high, with a minimum average per site of 1.73 in Tutakakahikura, and a mean of 2.44 across all sites. Pollination scores on female varied greatly between sites, ranging from 0.67 in Mount Sinclair to 3.80 in Oashore. Four sites had an average PLS per female *F. excorticata* tree below the threshold score of 1.5, indicative of insufficient pollination service (Robertson et al. 2008), and the mean of 1.56 across all sites was just above that threshold (Figure 3.1).

Of the parameters tested in single-factor models on pollen scores of hermaphrodites, only *F. excorticata* density had a significant effect, with an AIC lower than that of all the other models ($\Delta AIC > 13$ or higher) (Table 3.4). This is consistent with self-pollination ensuring hermaphrodites always get high pollen scores.

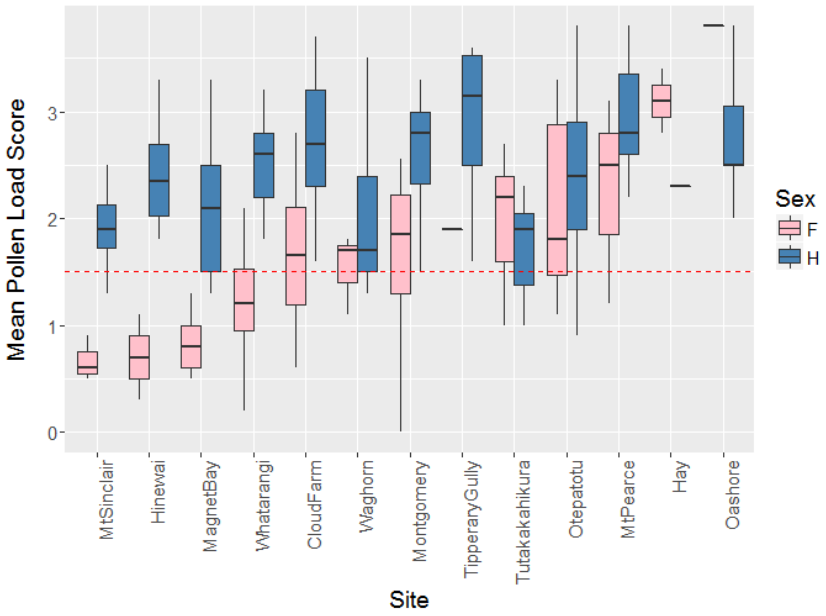

Figure 3.1: Boxplot of average pollen load scores (PLS) per site on female and hermaphrodite *Fuchsia excorticata* in 13 study sites, ordered by increasing values on females (data from 2013-14). Values below the red threshold line indicate insufficient pollination service (mean PLS < 1.5, Robertson et al. 2008).

Table 3.4: Analysis of variance table from the ANOVAs, with coefficients and standard errors from summary output of the generalized linear mixed models assessing the effects of altitude, area, dH, ADRA, edge, *F. excorticata* density, bellbird and silvereye densities on PLS of hermaphrodite *Fuchsia excorticata* flowers. Bold p-values indicate a significant effect (p < 0.1).

Response var.	Parameter	Coef.	Std. error	Df	Chisq.	p(>Chisq)	AIC
PLS	Intercept	0.9144	0.1254				
	Altitude	-0.0998	0.2428	1	0.1688	0.6811	4097.4
	Intercept	0.9897	0.1147				
	log(Area)	-0.0443	0.0387	1	1.3115	0.2521	4096.3
	Intercept	0.8734	0.0423				
	log(dH)	-0.0422	0.0429	1	0.9676	0.3253	4096.6
	Intercept	0.8551	0.0414				
	log(ADRA)	-0.0319	0.0226	1	2.0032	0.157	4095.7
	Intercept	0.8227	0.0529				
	Edge	0.0432	0.0291	1	2.2009	0.1379	4095.4
	Intercept (low)	1.0101	0.0696				
	FEdensity (med.)	-0.3497	0.0862				
	FEdensity (high)	-0.0758	0.0754	2	25.497	**<0.001**	**4082.3**
	Intercept	1.0073	0.1302				
	Bellbird	-0.0629	0.0553	1	1.2969	0.2548	4096.3
	Intercept	0.8153	0.0976				
	Silvereye	0.0303	0.0524	1	0.3344	0.5631	4097.2

A stepwise backward analysis was ran on the GLMM including only *F. excorticata* density as a fixed term effect, and the model selection suggested keeping this parameter in the final model, which output is presented in Table 3.5.

Table 3.5: Summary output of the selected GLMM testing the effect of *F. excorticata* density on the pollen load score of hermaphrodite *F. excorticata* flowers in 13 lowland forest sites on Banks Peninsula, taking into account the random effects of parent trees within sites. Bold p-values indicate a significant effect ($p<0.05$).

Generalized linear mixed model fit by maximum likelihood

Family	Poisson (log)				
Formula	*PLS ~ as.factor(FEDensity) + (1 | Site/TreeID)*				
Information criteria	AIC	BIC	logLik	deviance	df. residuals
	4082.3	4107.5	-2036.1	4072.3	1131
Scaled residuals	Min	1Q	Median	3Q	Max
	-1.7391	-0.6904	0.1965	0.7400	1.7187
Random effects	Groups	Name	Variance	Std. Dev.	Number of obs.
	TreeID:Site	(Intercept)	0.0203	0.1426	104
	Site	(Intercept)	<0.001	<0.001	13
					1136
Fixed effects		Estimate	Std. Error	z value	p(>|z|)
	(Intercept)	1.0101	0.0696	14.515	<0.001
	FEdensity (med.)	-0.3497	0.0861	-4.058	**<0.001**
	FEdensity (high)	-0.0758	0.0754	-1.005	0.315
Correlation of Fixed Effects		(Intercept)	FEdensity (med.)		
	FEdensity (med.)	-0.805			
	FEdensity (high)	-0.921	0.743		

On females, the models identified a significant negative effect of area and dH on pollination scores. The plotting of data was suggestive of a quadratic response of log(Area), with an initial increase in PLS with area followed by a decrease in the larger sites (Figure 3.2a). Connectivity index dH had no obvious trend on pollen load scores of females, but the two most connected reserves, which were also the largest, had low pollen load scores (Figure 3.2b).

The quadratic effects of Area and dH were tested in polynomial linear models using the formulas: *glm(formula = PLS ~ poly(log(dH),2), family = "poisson"*) and *glm(formula = PLS ~ poly(log(Area),2), family = "poisson")* to fit quadratic regression lines in the scatter plots. The analyses confirmed the observed curved response of female pollination scores to area, not to dH, so the quadratic effect of area was taken into account in the model selection process.

Table 3.6: Analysis of variance table from the ANOVAs, with coefficients and standard errors from summary output of the generalized linear mixed models assessing the effects of altitude, area, dH, ADRA, edge, *F. excorticata* density, bellbird and silvereye densities on PLS of female *Fuchsia excorticata* flowers. Bold p-values indicate a significant effect ($p < 0.1$).

Response var.	Parameter	Coef.	Std. error	Df	Chisq.	p(>Chisq)	AIC
PLS	Intercept	0.8115	0.3358				
	Altitude	-0.8656	0.6606	1	1.717	0.1901	2014.4
	Intercept	0.4091	0.0977				
	poly(log(Area))1	-5.6836	2.3927				
	poly(log(Area))2	-5.7461	2.2722	2	12.194	**0.0022**	**2008.9**
	Intercept	0.4431	0.1067				
	log(dH)	-0.3091	0.1183	1	6.830	**0.0090**	**2010.7**
	Intercept	0.3618	0.1263				
	log(ADRA)	-0.1242	0.0727	1	2.9193	**0.0875**	**2013.3**
	Intercept	0.4956	0.1330				
	Edge	-0.1719	0.1011	1	2.8903	**0.0891**	**2013.2**
	Intercept (low)	1.0424	0.2614				
	FEdensity (med.)	-0.9110	0.3249				
	FEdensity (high)	-0.6841	0.2995	2	8.0557	**0.0178**	**2011.4**
	Intercept	0.5036	0.4240				
	Bellbird	-0.0423	0.1747	1	0.0587	0.8086	2016.0
	Intercept	0.3897	0.3075				
	Silvereye	0.0102	0.1710	1	0.0036	0.9522	2016.1

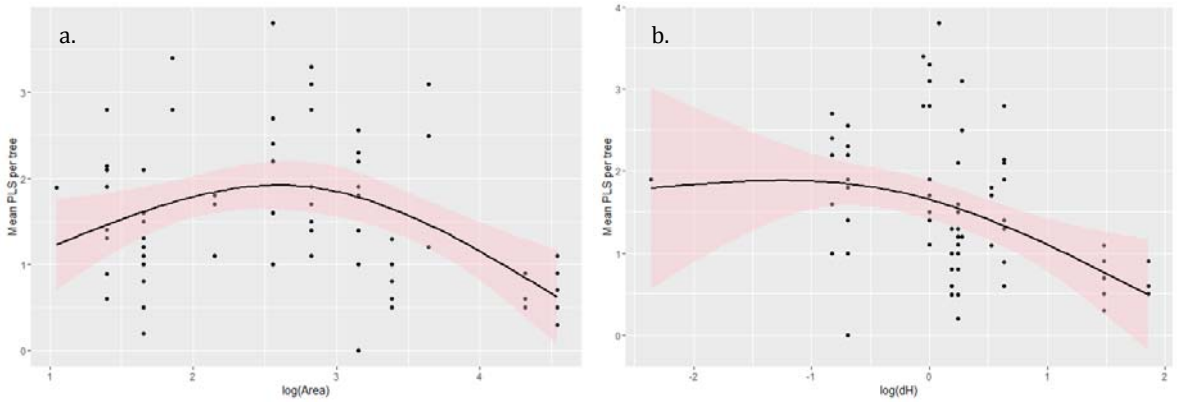

Figure 3.2: Scatter plot of pollen load scores (PLS) on female *Fuchsia excorticata* against (a) log(Area) and (b) log(dH), with fitted quadratic regression lines and confidence intervals (99 % confidence).

Five of the parameters tested in single-factor models on pollen scores of females had a significant effect ($p < 0.1$), with a $\Delta AIC < 5$ between these five models (Table 3.6). I ran the stepwise backward analysis on the initial GLMM including all five significant ($p < 0.1$) parameters using the formula: *glmer(PLS ~ poly(log(Area),2) + log(dH) + log(ADRA) + edge + as.factor(FEDensity) + (1|Site/TreeID) , control = glmerControl(optimizer = "bobyqa"), family = "poisson")*, including a control command to help the model converge.

The model selection suggested to drop edge and dH, and to keep the three other parameters: the final model with the lowest AIC included area, ADRA and FEdensity (Table 3.7).

Table 3.7: Summary output of the selected GLMM testing the effect of area, ADRA, and *F. excorticata* density, on the pollen load score of female *F. excorticata* flowers in 13 lowland forest sites on Banks Peninsula, taking into account the random effects of parent trees within sites. Bold p-values indicate a significant effect ($p < 0.05$).

Generalized linear mixed model fit by maximum likelihood

Family	Poisson (log)				
Formula	*PLS ~ poly(log(Area), 2) + log(ADRA) + as.factor(FEDensity) + (1 | Site/TreeID)*				
Information criteria	AIC	BIC	logLik	deviance	df. residuals
	1999.4	2035.0	-991.7	1983.4	627
Scaled residuals	Min	1Q	Median	3Q	Max
	-1.7277	-0.9244	0.0108	0.6873	2.8625
Random effects	Groups	Name	Variance	Std. Dev.	Number of obs.
	TreeID:Site	(Intercept)	0.0859	0.2930	60
	Site	(Intercept)	0.0031	0.0554	13
					635
Fixed effects		Estimate	Std. Error	z value	p(>|z|)
	(Intercept)	1.3908	0.2346	5.929	<0.001
	poly(log(Area))1	-3.6720	1.5517	-2.366	**0.018**
	poly(log(Area))2	-7.9094	1.4763	-5.358	**<0.001**
	log(ADRA)	0.1288	0.0525	2.453	**0.014**
	FEdensity (med.)	-1.3452	0.2769	-4.858	**<0.001**
	FEdensity (high)	-1.0096	0.2457	-4.108	**<0.001**

Correlation of Fixed Effects	(Int.)	p(log(A))1	p(log(A))2	Log(ADRA)	Fed(med.)
poly(log(Area))1	0.033				
poly(log(Area))2	-0.177	0.108			
log(ADRA)	0.622	-0.249	-0.238		
FEdensity (med.)	-0.912	-0.065	0.270	-0.606	
FEdensity (high)	-0.960	-0.014	0.165	-0.610	0.876

The fluctuation in pollination service between sites on female *F. excorticata* flowers was significantly correlated with a quadratic effect of area: there was an increase in mean PLS with area within small sites, and a decrease in PLS towards larger sites (Table 3.5). The model also identified a significant positive effect of ADRA and a significant negative effect of *F. excorticata* density on pollen load of females (Figure 3.3).

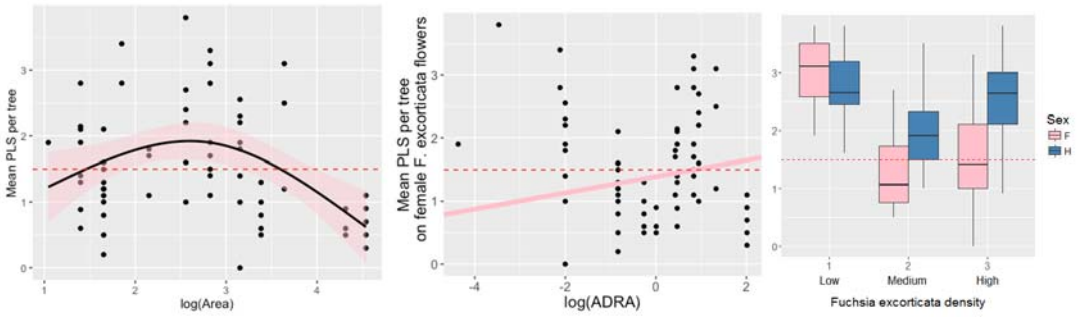

Figure 3.3: scatter plots with fitted regression lines and boxplot of the parameters kept by the model selection on the pollen load of female (pink) and hermaphrodite (blue) *F. excorticata* trees: (a) log(Area), (b) log(ADRA) and (c) *F. excorticata* density. Values under the red threshold line are considered showing insufficient pollination service (mean PLS < 1.5, Robertson et al. 2008).

IV. Discussion

High pollen loads on hermaphrodites

In the absence of visitation by birds, the ability of hermaphrodite *F. excorticata* flowers to self-pollinate ensures the production of a seed-set similar to that of cross-pollinated flowers (Robertson et al. 2011). In the 13 sites sampled for this study, pollen load scores on hermaphrodite flowers were always higher than the 1.5 threshold associated with sufficient seed-set (Robertson et al. 2008). There was little variation between sites, which is consistent with previous results in *F. excorticata* pollination studies throughout the country (Robertson et al. 2008; Iles & Kelly 2014).

The slight disparity in hermaphrodite pollination observed between sites was not explained by any of the site-level parameters tested in the model, and may be linked to local differences in herkogamy: self-pollination rates tend to increase in hermaphrodite *F. excorticata* flowers when the physical distance between the pollen bearing anthers and the receptive stigma decreases (Robertson et al. 2008). In populations with little herkogamy, hermaphrodite flowers are particularly prone to self-pollination, but self-pollinated seeds suffer high inbreeding depression, with reduced germination rates, limited seedling growth rates, and reduced survival rates with virtually no selfed individual persisting to the adult stage (Robertson et al. 2011). High pollen loads on hermaphrodite flowers are therefore not an indicator of successful pollination, but local differences in pollination between females and hermaphrodites may be suggestive of the importance of self-pollination within a population: when individuals of both sexes have equivalent pollen scores, it is likely that cross-pollination is occurring throughout the

population, whereas high pollen loads on hermaphrodites where females are lacking pollination service can be considered a signal of potentially high rates of self-pollination.

Pollination of females not affected by altitude or bird densities

The significant variation between sites in pollen loads on female *F. excorticata* flowers was not correlated with altitude, despite the significant influence of altitude on the density of flower visitors (Chapter 2). The model even found a nearly significant negative effect of local bellbird abundance, while silvereye had no effect on pollen loads. This result contrasts with previous studies on *F. excorticata*, which found that visitation rates and pollen scores on female flowers were significantly higher at sites with high pollinator densities and predator control (Robertson et al. 2008; Iles & Kelly 2014).

Successful pollination occurs when some pollen is transferred by a bird visitor from a hermaphrodite flower to flowers of either sex on other plants. Where mutualist bird are present in high densities, competition between and within species leads individual flower visitors to spend shorter time per plant and to visit more plants, meanwhile achieving effective cross-pollination (Anderson 2003), than at sites with low mutualist bird densities, where individual birds tend to spend more time on single plants, hence limiting the extent of their pollination service. On Banks Peninsula, the number of bellbirds detected per 5 min count was significantly higher in some sites than in others, generally increasing with patch connectivity and decreasing with altitude. The higher abundances of bellbirds were comparable to those recorded at some predator-free sanctuaries (local average of 2 bellbirds detected per 5 min count in Little Barrier Island, Kapiti Island, and Mapara Reserve, Murphy & Kelly 2001), with only three sites falling below the South Island East Coast mean of 1.36 bellbirds per count (Murphy & Kelly 2001). However, it is possible that the high numbers of bellbirds present in most of the study sites were proportionally not high enough to provide sufficient pollination service across most female plants of local *F. excorticata* populations. In a study assessing pollination and seed dispersal service by mutualist birds to native mistletoe species *Peraxila tetrapetala*, Kelly et al. (2004) found that bellbird densities required for adequate pollination were higher than for suitable dispersal service, hence the recurrence of pollination failure at sites with enough birds to achieve successful dispersal. On the other hand, high pollinator densities do not always result in the provision of sufficient mutualistic interactions: a restoration project on the extensively pollen-limited *P. tetrapetala* achieved significant increase in local bellbird abundance by 79% in 5 min counts after efficient predator control, but failed to restore adequate pollination service (Kelly et al. 2005).

Significant effect of area and connectivity on pollination of females

Area and connectivity index ADRA were both retained by the model selection process, area having a significant effect in the final GLMM on pollination service to female *F. excorticata* flowers. Local bird densities were positively affected by connectivity, with a positive effect of landscape-scale connectivity index dH specifically on bellbirds and silvereyes, while site-scale connectivity index ADRA was associated with increasing numbers of native forest birds such as kereru, tomtits and riflemen (Chapter 2). It is thus unsurprising that pollination service to female *F. excorticata* flowers was found to increase with connectivity: there was a positive effect of ADRA on polen load scores of females, supporting the importance of connectivity to pollination service on Banks Peninsula and consistent with similar findings in other studies (e.g. Lennartsson 2002; Cordeiro & Howe 2003; Cramer et al. 2007; Herrera & Garcia 2010). Although pollinator birds were more abundant at sites with higher dH, this parameter was not kept in the final model because of the confounding negative effect of large sites (which also had a high dH) on pollination.

Area had a quadratic response on pollen load scores, which increased significantly from small (< 5 ha) to medium-sized forest patches (about 15 ha), then decreased in larger sites. In small populations, reduced interplant movements of honeyeaters may limit the efficiency of flower visitors as pollinators (Harris & Johnson 2004). The enhancement of pollination service with increasing area is consistent with the widespread assumption that mutualistic interactions are improved where fragmentation effects are reduced (Wilcock & Neiland 2002). Behavioural responses of flower visitors vary between species, but there is evidence that even pollinators with high mobility and known ability to travel between distant patches tend to favour visits to nearby plants within a fragment (Harris & Johnson 2004). In large forest fragments, local *F. excorticata* pollinators are thus unlikely to fly away and feed in other patches, while pollinators from small neighbouring patches may reach the large fragments to complement their diet when local resources are insufficient. As a result, pollination service to female *F. excorticata* flowers was expected to increase with area until reaching a potential optimum above which pollen scores may remain high.

The decrease in pollination service observed in large areas was thus surprising, and was mostly caused by the low pollen loads measured in the two largest sites: Mount Sinclair (75 ha) and Hinewai (94 ha), where the two lowest local average pollen score per flower on female trees were recorded, respectively 0.67 and 0.7. Although unexpected, this result was consistent with Robertson et al. (2008) who also assessed pollination service in various sites throughout mainland New Zealand and recorded in Hinewai similarly low pollen scores on female flowers (mean pollen load of 0.5). Hinewai and Mount Sinclair were both mixed podocarp-broadleaf

forest remnants where *F. excorticata* was abundant, and where possum and rat populations were actively controlled. Native pollinator bird densities were as high as in pest-free bird sanctuaries (Murphy & Kelly 2001), exceeding an average of 2 bellbirds detected per 5-min count in both site (data 2005-16). In these large and conspicuous populations of *F. excorticata*, whose flowers are a preferred food source for the locally abundant bellbirds, the causes of an apparent pollination failure are still unknown, and require further exploration. Various studies have found that nectar feeding behaviour of honeyeater birds was directly related to food availability, with more flower visitations occurring on the larger inflorescences and among clustered flowering trees (e.g. Abrahamczyk & Kessler 2015). In Hinewai and Mount Sinclair, an important proportion of the flowering *F. excorticata* trees had few flowers accessible to the human hand (pers. obs.): in Hinewai most trees were tall with branches too high to reach by an observer, while in Mount Sinclair the understorey vegetation was so dense that the trees themselves were difficult to access through the forest. In both cases, the local configuration of the vegetation may favour nectar feeding by birds mostly high in the canopy, as commonly observed in other sites by Bell (2010). In this case, limited visits to flowers on the trunk and lower branches may explain the low average pollen scores recorded there. If technically possible, measuring pollen scores on both the canopy and the lower parts of female trees may allow for a more representative estimation of local pollination service in these two forest fragments.

Effects of vegetation structure on pollination of females: edge effect and F. excorticata density

In addition to local fragmentation measures such as patch area and connectivity level, some characteristics of the vegetation structure in a forest fragment have direct effects on the behavioural response of pollinator birds. In New Zealand native forests, bird communities vary a lot between forest interiors, where native species are more abundant, and forest edges, which are highly visited by exotic species from surrounding farmland (Barbaro et al. 2012). Changes in density and diversity of bird populations are known to affect competition and foraging behaviours (Pyke et al. 1977; Craig et al. 1981; Fontaine et al. 2008). In parts of New Zealand where bellbird and tui coexist in sufficient densities, the larger tui can defend flowering trees against the subordinate bellbird, which spends shorter times feeding on each plant, and is therefore more likely to achieve effective cross-pollination (Anderson 2003). On Banks Peninsula, where tui is only present as a small population (around 100-150 birds, Laura Molles pers. com.), such competitive behaviour is unlikely to occur.

In a literature review of published edge effects on plant-bird interactions in 85 plant species worldwide, Burgess et al. (2006) noted that the fruit or seed set of 50 plants was negatively affected by forest edge, while only 9 species had significantly higher fruit or seed set at the edge than in the forest interiors, including the declining New Zealand mistletoe *Peraxilla tetrapetala*. This unusual positive effect was related to higher flower visitation rates by insect and bird pollinators on *P. tetrapetala* plants at forest edges (Burgess et al. 2006). The reasons behind the preference of bellbirds in particular to feed on *P. tetrapetala* flowers at the edge were not known, but the authors suggested it may be due to a higher conspicuousness of flower displays in plain sunlight, and to the easier accessibility of inflorescences away from obstructing branches more commonly found in forest interiors (Burgess et al. 2006). For *F. excorticata*, there is a notable difference in tree physiognomy between individuals growing at forest edges and in forest interiors: forest trees are commonly tall with a large single trunk dividing into smaller branches close to the canopy, whereas "in more open situations […] the main trunk is less than 1 m tall and divides into several secondary trunks to form a large shrub up to 4 m high" (Godley & Berry 1995). This difference may involve easier access for bellbirds to *F. excorticata* inflorescences on forest trees than on shrubby individuals at forest edges.

Another factor known to affect pollinators' foraging behaviour is the local density of a plant population. For example, in a study comparing pollination service between various population sizes and spatial arrangements, individual *Lychnis viscaria* plants were receiving lower visitation rates, but bumblebee pollinators were spending longer durations feeding on flowers in sparse than in dense populations, irrespective of population size (Mustajarvi et al. 2001). Weber & Kolb (2013) found a similar pattern on visitation rates of bumblebees to the perennial herb *Phyteuma spicatum*. In the present study, among the 13 *F. excorticata* populations assessed for pollination, three consisted of trees sparsely scattered within the forest fragment, whereas in the other sites *F. excorticata* trees were present in remarkably higher densities. Pollen load scores were significantly higher at the three low-density sites. The foraging effort of *F. excorticata* pollinators may thus be limited by resource availability, favouring more thorough visitations of individual plants in sparse populations than in forest fragments where *F. excorticata* nectar wasn't a limited resource. This is consistent with Charnov's optimal foraging theory (1976), which predicts that in sparse populations, pollinators will feed on more flowers within a plant and move between flowering plants less often than when plant density is high. The apparent benefit of high pollen loads in sparse populations may however be limited by the reduced diversity of provisional pollen source, with cross-pollination probably occurring only between a few trees with a restricted genetic pool. In contrast, the drawback of lower pollination service in dense populations may be counterbalanced by an increased likelihood of effective cross-pollination per flower visitation: a number of studies

found that outcrossing rates were positively correlated with flowering plant densities, rather than with plant population area (e.g. Van Treuren et al. 1993; Mustajarvi et al. 2001).

V. Conclusion

The visual pollination scoring of *F. excorticata* flowers is a simple measure that allows for a reliable assessment of pollination service to flowering plants. Using a set of pollen load scores recorded in thirteen sites on female and hermaphrodite individuals across two consecutive flowering seasons on Banks Peninsula, I found that similarly to other studies (Robertson et al. 2008; Iles & Kelly 2014) hermaphrodite *F. excorticata* trees always carried pollen loads higher than the threshold average of 1.5 associated with sufficient seed-set. In contrast, there was a great variation on females between sites, with one third of forest fragments showing evidence of pollination failure. If the higher than average mean pollen score on hermaphrodites at low *F. excorticata* density sites appears to be linked with high geitonogamy (pollination from different flowers but within the same tree), then the next generation of hermaphrodites may suffer high inbreeding depression, and the locally high pollen scores on females may be masking this other type of pollination failure. Although pollination success is the direct effect of flower visitation by pollinator birds, pollen scores on females were not correlated with bellbird densities, neither with altitude which had a significant effect on the distribution of some bird species. However, pollination service increased with connectivity level, which also had a positive effect on bird densities. There was a significant effect of area on pollination service, which was increasing from small to medium-sized forest patches, then decreasing towards larger sites. This result suggests that the foraging behaviour of the mutualist birds present within a site is a more important factor for the provision of pollination service than local pollinator densities. Local vegetation structure is a factor influencing foraging behaviour of bellbirds, including *F. excorticata* density, and the location of flowering trees in a fragment. Edge effect was not significant in the combined model, whereas pollen loads were significantly higher at low *F. excorticata* densities.

The independence between local mutualist bird densities and bird feeding behaviour leading to variations in pollination service shows that the presence in seemingly sufficient number of two mutualist partners does not necessarily imply the successful achievement of the mutualistic interaction, as in Kelly et al. (2005). In well-connected sites where bellbirds are abundant and *F. excorticata* occurs in large populations, pollination success may be mistakenly assumed, and mutualism failure may remain unnoticed. In the present study, the pollen load

measurement method was well suited to assess pollination service on forest trees with enough accessible flowering branches, but less adapted to high canopy trees or trees embedded in dense understorey vegetation, as found in the two larger study sites. In sites with sparse populations, the high attractiveness of *F. excorticata* nectar led flower visitors to provide seemingly sufficient pollination service to all individuals, even where pollinators were not abundant. Increased movements within plants and reduced movements between plants in sparse populations are a common behaviour of insect pollinators (Mustajarvi et al. 2001), and my results seem to indicate it may be factual for honeyeaters as well. As foraging behaviour is limited by resource ability, other plants requiring mutualism with birds for reproduction may suffer from a lack of interaction where mutualist bird densities are low and nectar from *F. excorticata* flowers is present in sufficient supply to sustain the local population of flower visitors.

Based on these results, several factors should be taken into account when aiming to restore pollination service on a plant species: the flower attractiveness to pollinator in relation to other local food sources, the density of the plant population, and the density, diversity and competition pressure on its pollinators, which are influenced by patch connectivity. For *F. excorticata*, the sparse distribution of individuals in sites with low bird densities appeared to ensure the local persistence of adequate pollination service, which is expected to result in successful regeneration if local genetic structure hasn't been reduced and dispersal service allows for the deposition of seeds in suitable germination niches. Although sites with large populations of *F. excorticata* were apparently lacking pollination service on Banks Peninsula, further work will be needed to test for a potentially local predominance of high canopy foraging behaviour by pollinator birds, and to investigate alternative explanatory hypotheses if pollination service appears to be generally low regardless of inflorescence location within trees in large reserves.

CHAPTER 4:

Lowland forest fragmentation and seed dispersal service of *Fuchsia excorticata* on Banks Peninsula

Fuchsia excorticata fruits are green when unripe, dark purple when ripe and eatable.

(Photo Bushman Friends)

I. Introduction

Until human settlement in New-Zealand, a high proportion of the country was covered with forest, hence the unusually large representation of trees in the native flora (c. 240 species, or one third of all the native plant species) in comparison to other temperate countries (Atkinson & Cameron 1993). About 72% of this woody flora has fleshy fruits appropriate for dispersal by vertebrates; this is much higher than in comparable latitudes overseas where the fleshy-fruited flora accounts for less than half of the tree species (Burrows 1994).

In New Zealand, native vertebrate frugivores include several bird, bat and lizard species, which have often suffered great reduction in range and density following habitat loss and predation by introduced mammals. Out of the two endemic short-tailed bat species that were feeding on fruits, one has become extinct (*Mystacina robusta*), while the other (*M. tuberculata*) has been drastically reduced, and its population is still declining (Lloyd 2001). There has been evidence that lizards can act as effective seed-dispersers over short distances, and their dispersal service is of particular importance in shrublands lacking frugivorous birds, however their contribution to dispersal has also been severely limited by important declines in population densities (Towns et al. 2001; Wotton et al. 2016). Plants whose fruits were consumed by lizards appear to be equally visited by birds, which are able to provide dispersal service over longer distance (Thorsen et al. 2009; Wotton et al. 2016). Incidental consumption of small fruits by invertebrates, such as *F. excorticata* berries by the tree weta, doesn't occur at sufficient rates and with significant efficiency to replace the role of birds in seed dispersal (Wyman et al. 2011). It has been suggested that introduced mammals may participate in seed dispersal, with some records of contribution by rats, possums and feral pigs on the dispersal of a few plants, however this incidental benefit is largely outdone by their mostly destructive consumption of seeds, and by their negative effect on the density of birds that remain the most efficient dispersers for these plants (Kelly et al. 2006). Similarly, large exotic herbivores such as goats, sheep, cows and horses may accidentally ingest the seeds of some native plants while browsing on the foliage, which could potentially result in effective dispersal events, however the detrimental effect of browsing on the regeneration of these native plants is likely to surpass any successful dispersal event (Burrows 1994; Kelly et al. 2006; Wyman 2013).

New Zealand fruits have been reportedly eaten by 31 bird species, including some that only incidentally added fruits to their mainly insectivorous diet (nine native and six exotic bird species in Kelly et al. 2006), and some that acted primarily as seed predators rather than effective dispersers, especially native parrots such as kea, kaka, red-crowned parakeet, and yellow-crowned parakeet (Clout & Hay 1989). Among the native avifauna, 11 bird species have

been identified as formerly important dispersers of New Zealand seeds, including four species that are now extinct: huia, piopio, and two moa species (Holdaway 1989). Four other species have been severely range-restricted in abundance and distribution: saddleback and stitchbird, which only remain in predator-free (mainly offshore) bird sanctuaries, and kokako and weka, which are now both uncommon on the mainland (Anderson et al. 2006). That leaves only three widespread native bird species to participate in seed dispersal throughout the country: kereru, tui, and bellbird, which have all been reduced in densities, some of them being locally absent in various parts of the mainland (Anderson et al. 2006). However, birds are widespread and abundant even where native birds are lacking, and five species have been reported to disperse seeds effectively: the naturalized silvereye, and exotic blackbird, song thrush, common myna (*Acridotheres tristis*), and starling (O'Donnell & Dilks 1994). In Banks Peninsula forest remnants, Burrows (1994) showed that blackbird and silvereye were now the main seed dispersers of various native plants. However, when considering the fruit consumption of 32 native plant species, Kelly et al. (2006) found that blackbird only accounted for 3.9% of all fruit visitations, whereas kereru, tui, bellbird and silvereye were together responsible for 83.7% of all fruit visitations.

The general decline in disperser diversity, density and distribution throughout New Zealand has raised concerns about the potential for dispersal failure in some native plants. Five native species have large fruits (> 1.4 cm in diameter) that rely on kereru for dispersal (Clout & Hay 1989). Kokako and tui have been reportedly eating large fruits (up to 2.1 cm in diameter), including fruits smaller than average in the six largest fruited species (Kelly et al. 2010). Despite their smaller gape sizes, bellbird and blackbird are able to swallow fruits with a diameter up to 1.3 cm, and silvereye can swallow fruits of up to 9.9 mm in diameter (Kelly et al. 2010). The three species are also highly mobile while feeding, hence potentially achieving efficient dispersal, whereas the more sedentary kereru eats fruits of all sizes and has restricted movements while feeding, but also has a long gut passage time allowing for ingested seeds to be dispersed away from the parent (Burrows 1994; Wotton & Kelly 2012). Although Kelly et al. (2010) showed that for several large and medium-sized fruits in the native flora, the absence of ingestion by a frugivore was not preventing germination, and New Zealand species were generally little affected by Janzen-Connell effects (Wyman 2013), Wotton & Kelly (2011) found that for two large-seeded native tree species, *Beilschmiedia tarairi* and *Corynocarpus laevigatus*, dispersal failure had a negative impact on germination, seedling growth and survival rate, with strong synergetic effects off mammalian seed predation. Various studies have found evidence that seed dispersal service was sometimes inadequate at mainland sites with low native frugivore densities, compared to offshore sites in bird sanctuaries, despite the presence in high

abundance of introduced birds on the mainland (Anderson et al. 2006; Wyman 2013). Yet, Kelly et al. (2010) found that dispersal seemed to be failing in only one out of 11 tree species tested.

In the context of forest fragmentation, landscape connectivity is an important factor affecting the densities of mutualist bird species. Because of the relatively higher diversity and density of disperser vs. pollinator bird species in New Zealand, and because dispersal service can sometimes be achieved at mutualist densities that appear insufficient for adequate pollination (Kelly et al. 2004), seed dispersal is considered to be less at risk than pollination (Anderson et al. 2006). However, the conditions required to restore disrupted pollination are not necessarily suited for the restoration of seed-dispersal; in fact Kaiser-Bunbury et al. (2010) argued that once disrupted, the requirements for re-establishing successful dispersal may be more difficult to meet than for pollination. Where frugivore birds are present in low densities, high-reward plant species are preferred for consumption, leaving plants with fruits of lower nutritional values at greater risk of dispersal failure (Anderson et al. 2006; Wyman 2013). Some important aspects of seed dispersal to plant reproduction include the contribution to gene flow within and between populations, thus limiting inbreeding depression, and the potential to allow for species recruitment and long-term persistence in isolated fragments (Sekercioglu et al. 2004; Kaiser-Bunbury et al. 2010; Wotton & Kelly 2011).

Fuchsia excorticata is a native tree that regenerates in disturbed environments, therefore seed dispersal to suitable microsites may be particularly important for this species to persist (Robertson et al. 2008; Bell 2010). However, it produces considerable seed banks and the seeds have the ability to enter in a dormant state, so germination can be delayed until environmental conditions become suitable (Burrows 2007). *Fuchsia excorticata* fruits are small multi-seeded berries commonly eaten by various bird species. In a South Westland forest, kereru were responsible for 64.1%, blackbird 17%, silvereye 11.7%, bellbird 4.8%, and fantail 2.4% of all observed fruit visitations by birds to *F. excorticata* berries (O'Donnell & Dilks 1994, listed in Kelly et al. 2006). On Kapiti Island, where native frugivore bird densities are high, tui and bellbird were the most common birds observed feeding on *F. excorticata* fruits, whereas on the South Island it has been suggested that the high abundance of blackbirds around Dunedin may be responsible for the increase in *F. excorticata* population in the Town Belt (Godley & Berry 1995). Although bellbirds are known to consume *F. excorticata* fruits, these do not appear to be among their preferred food. Spurr et al. (2011) found that between the various plant species visited by bellbirds for fruit consumption, *F. excorticata* was used less than expected in relation to its availability, and was mostly consumed during the short transition between the seasonal foraging on *F. excorticata* nectar to the fruit ripening of other plant species, which were in contrast visited more than expected given their availability. On Banks Peninsula, tui

abundance in forest fragments is too low (Chapter 2) to have a detectable effect on the consumption and potential seed dispersal of *F. excorticata* berries. The incidental foraging on *F. excorticata* fruits by the insectivorous fantail is also unlikely to affect seed dispersal. Therefore, local bird species that may provide efficient dispersal service to *F. excorticata* seeds only include bellbird, blackbird, kereru and silvereye. In a study comparing fruit removal rates between sites of various bird abundances, Robertson et al. (2008) found that the proportion of ripe *F. excorticata* berries remaining on a branch, indicative of non-dispersal, was higher on the mainland than on a pest-free island with high frugivore densities. In addition to bird abundances, *F. excorticata* population density had a positive effect on seed dispersal rates (Bell 2010).

In Chapter 2, I found that the four species of frugivore birds known to feed on *F. excorticata* fruits were significantly more abundant in well-connected forest fragments, but their densities decreased with area. In this chapter, I aimed to identify which fragmentation parameters were significant predictors of seed dispersal service to *F. excorticata*. I compared the factors influencing *F. excorticata* fruit consumption with those affecting mutualist bird distributions to detect the importance of each bird species for *F. excorticata* dispersal. I intended to infer an estimation of local bird density requirements for sufficient dispersal service.

II. Methods

Dispersal service

Fuchsia excorticata is a fleshy-fruited native forest tree, with ripe berries that are a preferred food for several bird species during the fruiting season, typically lasting from late spring to early autumn (O'Donnell & Dilks 1994; Godley & Berry 1995). A seed dispersal index that can be measured in single visits has been developed by Robertson et al. (2008) for the assessment of dispersal service to *F. excorticata*. In summer, the proportion of ripe or overripe fruits remaining on a tree (i.e. not consumed by a mutualist bird) was highly correlated to fruit removal rates (Robertson et al. 2008). Sites in which more than 40% of all *F. excorticata* fruits were ripe (or less than 60% of all fruits were green) were considered as lacking dispersal service (Robertson et al. 2008).

Dispersal index of *Fuchsia excorticata* trees was measured at ten sites during summer 2013-14, from usually 10 trees per site in eight sites (four trees in Tipperary Gully where the fruiting *F. excorticata* population was low, and five trees in Waghorn where the number of

accessible fruiting adults was limited; Table 4.1). The total number of fruits on a branch (up to 78 fruits per branch, average = 39.4) and the number of green fruits on the same branch were used to calculate a fruit removal index by dividing the number of green fruits present on a branch by the total number of fruits on that branch. This fruit removal index was positively correlated with seed dispersal service: when the proportion of green fruits is low, most fruits on the tree are ripe, which is a reliable indicator of poor dispersal service (Robertson et al. 2008); when the proportion of green fruits is high, most ripe fruits have been consumed and their seeds potentially dispersed by birds, demonstrating sufficient dispersal service.

Site-specific parameters: biotic and abiotic factors

The successful dispersal of *F. excorticata* seeds is directly related to fruit consumption by efficient dispersers. On Banks Peninsula, *F. excorticata*'s main dispersers are affected in various ways by forest fragmentation, usually decreasing in density with altitude and area, and increasing significantly with connectivity (landscape-scale connectivity index dH for bellbird, silvereye, and total dispersers, and site-scale connectivity index ADRA for kereru).

The frugivores' foraging behaviours may also be influenced by local vegetation structures, including edge effects and site-specific *F. excorticata* densities. Edge effect was recorded as a factor, with trees sampled either at the edge (E) or at the interior (F, under close canopy at least 5 m from the edge) of the forest fragments. *Fuchsia excorticata* density wasn't measured quantitatively at the time of the experiment, so I used a subjective population density scale of 1 to 3 based on personal field observations, which estimates visually the proportion of *F. excorticata* in the overall canopy cover of each site within the area where fruit removal was measured: (1) low *F. excorticata* density with less than 10% of the canopy cover, (2) medium density with 10-40% of the canopy cover, and (3) dominant species making over 40% of the canopy cover.

To determine which factors were significant predictors of the dispersal service of *F. excorticata* seeds, I tested the effects of altitude, area, dH, ADRA, edge, *F. excorticata* density, and mean number of disperser birds detected per count (including bellbird, blackbird, kereru, and silvereye, data 2005-16) on local Dispersal Index. For each study site where dispersal indices were measured, the number of trees sampled, and other relevant site chracteristics are presented in Table 4.1.

Table 4.1: Characteristics of sites used for dispersal: number (n) of fruiting *Fuchsia excorticata* trees measured for percentage of green fruits during summer 2013-14, local average DI per tree, altitude, area, dH value, importance of *F. excorticata* in the forest canopy, and average number of frugivore birds (bellbird, blackbird, kereru, and silvereye) detected per 5-min count (data 2005-16) in 10 lowland forest fragments on Banks Peninsula.

Site	n	% green fruits	Alt. (m)	Area (ha)	ADRA ($ha.m^{-1}$)	dH (%)	*F. exc.* density	Bellbird	Blackbird	Kereru	Silvereye
Cloud Farm	10	76.14	620	4.05	1.60	1.88	3	2.65	1.24	0.47	2.65
Hinewai	10	37.17	400	93.44	7.48	4.39	3	2.31	1.23	0.58	0.88
Magnet Bay	10	30.71	240	29.49	0.77	1.21	2	0.94	0.94	0.35	1.12
Montgomery	10	48.77	500	23.38	0.13	0.50	3	2.83	0.98	0.15	2.29
Mt Sinclair	10	68.84	740	74.72	1.01	6.40	2	2.08	1.08	0	2.46
Otepatotu	10	60.08	660	16.84	2.30	1.00	3	1.81	1.31	0.34	0.75
Tipperary Gully	4	10.52	300	2.84	0.01	0.09	1	0.35	1.76	0	2.41
Tutakakahikura	10	48.01	380	12.89	2.57	0.44	2	2.09	0.45	0.64	1.91
Waghorn	5	51.41	680	8.60	1.53	1.69	2	3.25	0.58	0.08	0.58
Whatarangi	10	51.07	580	5.22	0.43	1.27	3	2.65	0.88	0.06	2.12

Statistical analyses

All statistical analyses were performed using the program R version 3.1.1 (R Core Team 2014). The dispersal index was computed in R using a *cbind* command, which combined the number of green fruits and the number of ripe fruits for each branch sampled, while allowing for data structure by taking into account the variation between samples in total fruits counted per branch. An average dispersal index per site was calculated from a total of 89 records in 10 sites. Dispersal index was overdispersed, so the analyses were performed using a quasibinomial error distribution. I tested the effect of site on dispersal index (Table 4.2) using a quasibinomial generalized linear model (*glm* command in R) with the formula: *glm(formula = %green ~ Site, family = quasibinomial)*.

To identify which site-specific parameters may explain this variation on *F. excorticata* dispersal success, I used the raw dataset of 89 dispersal index values to run ten single-factor generalized linear mixed models (GLMM) with binomial error distribution (*lme4* package in R), allowing for data structure by including a random term for tree within site, and analysed with an ANOVA based on Chi-squared test (*Anova* command from *car* package in R).

I used the formula: *glmer(formula = DI ~ x + (1|Site/TreeID), family = "binomial")*, where the explanatory variable x was respectively altitude, area, connectivity indices dH and ADRA, edge, *F. excorticata* density, mean number of bellbird, silvereye, blackbird and kereru detected per count. Area, dH and ADRA were log-transformed in order to increase the normality of their

distribution across data.

All parameters with a individual effect significant at p<0.1 were then included in a model selection process, starting with a new GLMM with binomial error distribution and a random term for tree within site, then manually removing fixed-effect parameters one at a time (*drop1* command in R, with *test = "Chisq"*). This stepwise backward model selection was repeated until no parameter elimination would decrease further the model's AIC. The final model best explaining the data was then analyzed with an ANOVA based on Chi-squared test.

III. Results

Local percentage of green fruits on *Fuchsia excorticata* fruiting trees was significantly variable between sites ($p < 0.001$, Table 4.2), ranging from a minimum of 10.5 % in Tipperary Gully to a maximum of 76.1 % in Cloud Farm (Table 4.1). Only 3 sites had most of the sampled trees over the threshold of 60% green fruits indicating sufficient dispersal service (Figure 4.1).

Table 4.2: Analysis of deviance table from the GLM assessing the effect of site on the dispersal index (DI) of *Fuchsia excorticata* trees. Bold p-values indicate a significant effect ($p < 0.05$).

Response variable	**Parameter**	**Df**	Deviance	Resid. Df	Resid. Dev	p(>F)
% green fruits	NULL			88	668.65	
	Site	9	345.37	79	323.28	**< 0.001**

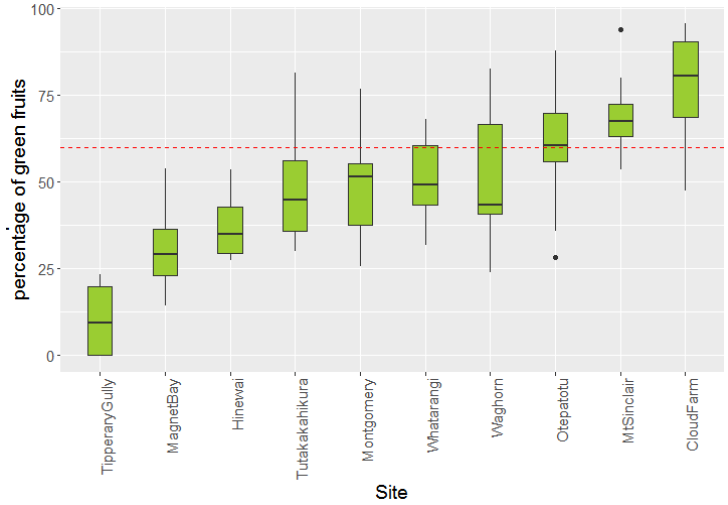

Figure 4.1: Percentage of green fruits per *Fuchsia excorticata* tree in 10 lowland forest fragments, ordered by increasing local average values (data from summer 2013-14). Values below the red threshold line indicate insufficient dispersal service (mean < 60 %, Robertson et al. 2008).

The models identified a significant (p<0.1) effect of altitude, dH, ADRA, FEdensity and Bellbird on dispersal index, with a ΔAIC < 10 between these five models (Table 4.3).

Table 4.3: Analysis of variance table from the ANOVAs, with coefficients and standard errors from summary output of the generalized linear mixed models assessing the effects of altitude, area, dH, ADRA, edge, *F. excorticata* density, bellbird, silvereye, blackbird and kereru densities on Dispersal index of *Fuchsia excorticata* trees. Bold p-values indicate a significant effect (p < 0.1).

Response var.	Parameter	Coef.	Std. error	Df	Chisq.	p(>Chisq)	AIC
DI	Intercept	-2.0000	0.4830				
	Altitude	3.9253	0.8875	1	19.561	**<0.001**	**574.5**
	Intercept	-0.1636	0.6891				
	log(Area)	0.0507	0.2328	1	0.0475	0.8275	585.6
	Intercept	-0.0865	0.2173				
	log(dH)	0.4410	0.1992	1	4.8989	**0.0268**	**581.3**
	Intercept	0.0312	0.2283				
	log(ADRA)	0.2662	0.1429	1	3.4686	**0.0625**	**582.4**
	Intercept	-0.0250	0.2653				
	Edge	0.0015	0.1563	1	<0.001	0.9921	585.6
	Intercept (low)	-1.9943	0.7495				
	FEdensity (med.)	2.0072	0.8098				
	FEdensity (high)	2.2458	0.7967	2	7.9484	**0.0188**	**581.0**
	Intercept	-1.3524	0.8111				
	Bellbird	0.5783	0.3361	1	2.9600	**0.0853**	**582.8**
	Intercept	-0.4124	0.6114				
	Silvereye	0.2284	0.3277	1	0.4858	0.4858	585.2
	Intercept	0.6218	0.8033				
	Blackbird	-0.6250	0.7402	1	0.7129	0.3985	584.9
	Intercept	-0.1411	0.4009				
	Kereru	0.4264	1.1223	1	0.1443	0.7040	585.5

I ran the stepwise backward analysis on the initial GLMM including all five significant (p<0.1) parameters using the formula: *glmer(DI ~ Altitude + log(dH) + log(ADRA) + as.factor(FEDensity) + Bellbird + (1|Site/TreeID), control = glmerControl(optimizer = "bobyqa"), family = "binomial")*, including a control command to help the model converge.

The model selection suggested dropping ADRA, dH and bellbird density, and keeping the two other parameters. The final model with the lowest AIC included altitude and FEdensity, which both had a significant effect on dispersal index (Table 4.4).

Table 4.4: Summary output of the selected GLMM testing the effect of altitude and *F. excorticata* density, on the proportion of green fruits per branch on *F. excorticata* branches in 10 lowland forest sites on Banks Peninsula, taking into account the random effects of parent trees within sites. Bold p-values indicate a significant effect ($p < 0.05$).

Generalized linear mixed model fit by maximum likelihood

Family	Binomial (logit)				
Formula	*DI ~ Altitude + as.factor(FEDensity) + (1 | Site/TreeID)*				
Information criteria	AIC	BIC	logLik	deviance	df. residuals
	573.7	588.6	-280.9	561.7	83
Scaled residuals	Min	1Q	Median	3Q	Max
	-1.0966	-0.3257	-0.0469	0.2666	1.3810
Random effects	Groups	Name	Variance	Std. Dev.	Number of obs.
	TreeID:Site	(Intercept)	0.3775	0.6145	89
	Site	(Intercept)	0.0849	0.2915	10
					89
Fixed effects		Estimate	Std. Error	z value	p(>|z|)
	(Intercept)	-2.9671	0.6281	-4.724	**<0.001**
	Altitude	3.2720	0.8166	4.007	**<0.001**
	FEdensity (med.)	1.3461	0.6296	2.138	**0.0325**
	FEdensity (high)	1.4131	0.6344	2.227	**0.0259**
Correlation of Fixed Effects		(Intercept)	Altitude	FEdensity(med.)	
	Altitude	-0.393			
	FEdensity (med.)	-0.744	-0.255		
	FEdensity (high)	-0.711	-0.322	0.918	

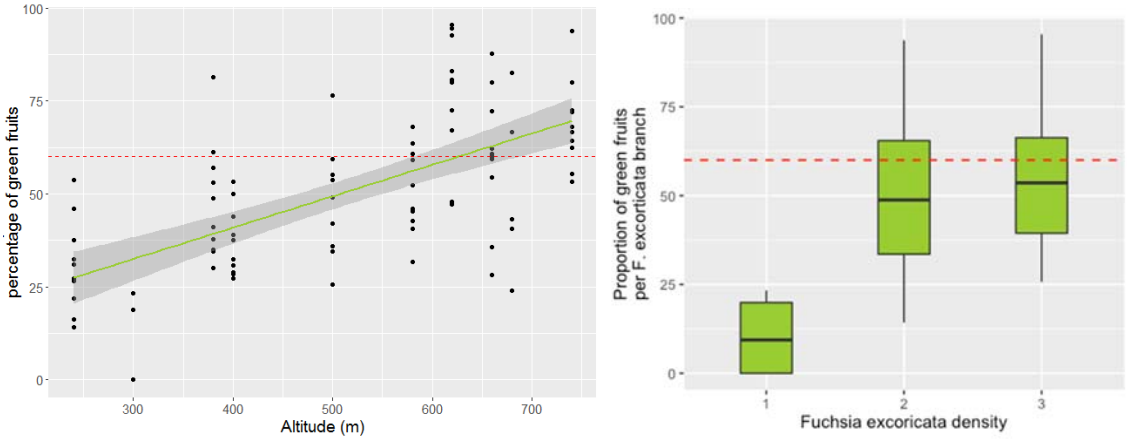

Figure 4.2: scatter plot with fitted regression line and boxplot of the parameters kept by the model selection on the number of green fruits remaining per *F. excorticata* branch: (a) Altitude, and (b) *F. excorticata* density. Values under the red threshold line are considered showing insufficient dispersal service (green fruits < 60 %, Robertson et al. 2008).

IV. Discussion

Effect of bird densities on dispersal service

Four bird species are known to consume *F. excorticata* berries and were present in Banks Peninsula's forest fragments in sufficient numbers to be potentially responsible for *F. excorticata* seed dispersal.

Kereru are able to fly long distances between patches, making virtually no forest fragment totally isolated for a kereru to reach on Banks Peninsula, and tend to alternate between long feeding times and long resting times. Large kereru meals of *F. excorticata* berries would certainly result in significantly low percentages of ripe fruits left where it is present. In a South Westland forest, Kereru was thus found to achieve c. 64% of all *F. excorticata* fruit consumption (O'Donnell & Dilks 1994, listed in Kelly et al. 2006). In contrast, there was no correlation between kereru abundance and *F. excorticata*'s green fruit percentage in my study. Among the 10 lowland forest patches used in this experiment, kereru was never detected (data 2005-16) in two sites: Mount Sinclair and Tipperary Gully, where the local average green fruit percentage was respectively high (68.84%) and low (10.52%). Tutakakahikura, where kereru was detected the most in 5-min bird counts, had a mean green fruit percentage of 48%. Given the frequent lack of conspicuousness of kereru, which tend to remain silent and steady for long time intervals, 5 min counts may lead to poor estimations of their local densities, almost entirely based on individuals seen during the counts. As a consequence, no link can be established with certainty between local kereru abundance and fruit removal of *F. excorticata* berries on Banks Peninsula.

Primarily nectarivores, bellbirds are known to include some fruits and invertebrates in their diet, including *F. excorticata* berries, however these are not a preferred food source. During the *F. excorticata* fruiting season, which can extend from late spring to early autumn, bellbirds were found to feed preferentially on other native plants producing fruits or still flowering, such as the latest seasonal *F. excorticata* flowers and fruits of the red matipo (*Myrsine australis*), which in another study were consumed in proportions higher than would be expected from their spatial availability alone (Spurr et al. 2011). In contrast, *F. excorticata* fruits seemed to be a less preferred food source, and were consumed by bellbird less frequently than expected from their availability, except when food was a limiting resource because of high competition: e.g. on Kapiti Island, where native bird densities are high, bellbirds were reported to eat *F. excorticata* fruits even before they had ripened (Godley & Berry 1995). In a South Westland forest, bellbirds were responsible for less than 5% of all consumption of *F. excorticata*

fruits (O'Donnell & Dilks 1994, in Kelly et al. 2006). In my study, bellbird density had no effect on the Dispersal Index of *F. excorticata*.

Silvereye and blackbird are more generalist birds, also known to eat *F. excorticata* berries (respectively 11.7% and 17% of all *F. excorticata* fruit visits in a South Westland site; O'Donnell & Dilks 1994, in Kelly et al. 2006). An observed increase in *F. excorticata* abundance around Dunedin in the early 1900s was suggested to have resulted from an increase in blackbird densities (Godley & Berry 1995). In my study, there was no significant relationship between the proportion of fruits eaten on *F. excorticata* trees and the average number of blackbird or silvereye detected per count. However, Burrows (1994) showed that on Banks Peninsula, blackbird and silvereye were currently the most important species for seed dispersal of various native plants. As a flocking species, silvereye tend to be either counted as absent or present as more than one individual, therefore its density fluctuates with greater variation than non-flocking birds. Silvereyes are also highly mobile birds that keep moving while feeding, and which are commonly found in equal densities in native forest patches and in mixed farmland habitat plots (Deconchat et al. 2009). The consumption of *F. excorticata* fruits by a flock of silvereyes is thus likely to result in potentially high fruit removal rates, and in the deposition of seeds away from parent trees. *F. excorticata* requires seed deposition into suitable, usually disturbed habitats to regenerate (Robertson et al. 2008; Bell 2010), which may be effectively facilitated by silvereye's foraging behaviour and habitat range.

Dispersal service is independent from edge effect and F. excorticata density

The significant variation between sites in the proportion of green fruits on *F. excorticata* trees was not significantly affected by *F. excorticata*'s relative importance in local foliage cover, and there was no significant difference in fruit removal between trees located at the edge and trees located at the core of the forest fragments. Both parameters were shown in Chapter 3 to affect pollinators' foraging behaviour, with significantly higher pollen loads on female flowers in forest interiors, and in sites with sparse flowering trees.

In a study assessing edge effects on avian assemblages in native forest fragments of Banks Peninsula, silvereye was detected in higher abundances in edge plots than in forest interior plots (Barbaro et al. 2012). As silvereye densities were significantly affecting fruit removal of *F. excorticata* berries in my study sites, the lack of significant difference between the proportion of green fruits recorded on trees located at the edge and at forest cores indicates that silvereye's foraging behaviour was not influenced in any direction by a potential edge effect. On the contrary, regardless of bird densities, the presence of frugivorous birds inside

forest patches was frequent enough to provide equivalent seed dispersal service to trees located at any given location of a particular patch.

The positive effect observed for *F. excorticata* density on the local proportion of green fruits was not significant in the model. Among the ten sites in which I measured green fruit percentages, only one had a scarce *F. excorticata* population, in which there was a significantly lower proportion of green fruits than in sites with denser populations of fruiting *F. excorticata* trees. This is consistent with the results in Bell (2010), who found that *F. excorticata* seed dispersal rates were increasing with *F. excorticata* densities.

Is F. excorticata dispersal actually failing in elevated and isolated fragments?

Based on comparisons between bird-depleted mainland sites and a pest-free island where frugivores were abundant, Robertson et al. (2008) estimated that *F. excorticata* seed dispersal service could be considered successful when the proportion of ripe fruits remaining on a branch were below 40%, i.e. when the percentage of green fruits was higher than 60%. Among the ten sites surveyed in my study, such a suitable dispersal service was only provided at three sites. When extrapolating from the coefficients produced by the generalized linear model, successful dispersal of *F. excorticata* seeds would only be achieved above a threshold altitude of 600 m, or a threshold patch connectivity level of dH > 4.5 (i.e. log(dH) > 1.5), with virtually no silvereye densities currently high enough in any of the study sites. This alarming result should be taken with caution. Altitude is known to influence the annual start and length of *F. excorticata* flowering season, with usually later and longer flowering seasons occurring at higher altitudes (Bartholomew 2008). As a consequence, fruits are being produced and start ripening earlier at low altitudes than at higher altitudes where comparatively warm temperatures are reached later in the summer. Field measurements of green fruit percentages were all carried out within a few weeks, when *F.* excorticata trees in my study sites were all fruiting, however due to altitudinal differences the most elevated sites may have been less advanced in the fruit ripening season. Thus, the lower proportion of green fruits found at low altitudes is likely due to the combination of an actual lack of dispersal service by birds and the survey being carried out relatively late in the fruiting season, when no more green fruits were being produced. In contrast, sites located at higher altitudes had larger proportions of green fruits not only because ripe fruits were being removed at higher rates, but also because the survey was carried out relatively early in the fruiting season there so a comparatively low proportion of the local fruits had ripen. The implication of this altitudinal difference in ripening period is a possibly overestimated variation in dispersal service between sites along the

altitudinal gradient: the apparent lack of dispersal service in low altitude patches may not be as severe as it seems, and the seemingly high fruit removal rate estimated in the most elevated patches may not be as important as the local proportion of green fruits indicates.

On the other hand, forest fragment isolation, estimated here based on the importance dH of the contribution of each patch to the overall landscape connectivity, is independent from altitude and seasonal weather conditions, and has a significant effect on both mutualist bird densities (Chapter 2) and *F. excorticata* fruit removal, but not on pollination service (Chapter 3). In Tipperary Gully, the most isolated patch among the ten study sites, fruiting *F. excorticata* trees had an average of only 10% of green fruits, so 90% of the fruits were undispersed at the time of the survey, indicating severe mutualism failure. (Bond 1994) discussed the importance of three factors in estimating local plant species extinction risk from mutualism failure, named in Kelly et al. (2004) "mutualist service", "mutualist-dependence", and "seed-dependence." Mutualist service depends on the diversity and level of specialization of the mutualist species involved, and can be measured for dispersal service as fruit visitation rate. As *F. excorticata* fruits have a relatively long life span, and are known to be consumed by at least four common frugivorous birds on Banks Peninsula, including two widespread generalists (blackbird and silvereye), the risk of poor mutualist service for *F. excorticata* can be considered moderate. Mutualist-dependence of *F. excorticata* reproduction depends for dispersal service on the reliance of seed dispersal on mutualist birds. (Burrows 1995) found that 96% of *F. excorticata* seeds germinated after being cleaned, watered and kept in a well-lit environment, but no germination from intact fruits kept in petri dishes, from which any inhibiting chemicals could not leach away (Robertson et al. 2006). However, in complementary germination trials from whole fruits of three bird-dispersed fleshy-fruited species, seeds in intact fruits that were unable to germinate in the petri dishes had successful germination rates both in the field and in potting mix experiments (Robertson et al. 2006). As the passage through a bird's gut isn't necessary for *F. excorticata* seeds to germinate, and the number of seeds per fruit is high, but the proportion of dispersed seeds deposited by birds into suitable niches for successful establishment remains unknown, mutualist dependence of *F. excorticata* dispersal service can also be considered moderate. Seed-dependence of population maintenance refers to the rate of successful dispersal required for long-term persistence of plant populations, and is usually low for long-lived and pioneer species such as *F. excorticata*, which produces important persistent seed banks (Bell 2010), has high germination rates, and is able to colonize disturbed environments (Burrows 1995; Godley & Berry 1995; Robertson et al. 2008). None of the three risk factors described by Bond (1994) seem to rank highly for seed dispersal of *F. excorticata,* therefore dispersal failure alone is unlikely to result in local extinction, but may be of greater concern when occurring conjointly with pollination failure.

Individual effects of area and connectivity on dispersal service

As the strong correlation between altitude and Dispersal Index may have biased the model selection process, it is interesting to have a complementary look at the results of single-predictor models. The models testing individually the effects of various parameters on the proportion of green *F. excorticata* fruits found a significant increase with increasing landscape-scale connectivity index dH, but no effect of area. In Chapter 2, I found that on Banks Peninsula the guild of disperser birds (i.e. bellbird, blackbird, silvereyes and kereru) was significantly decreasing in density with increasing area, while patch connectivity had a positive effect on all native frugivores. These results are consistent with previous studies from overseas, which recorded the presence of fewer frugivorous birds and the occurrence of lower fruit dispersal service in isolated fragments than in continuous forests.

Studies assessing the effects of forest fragmentation on seed dispersal of ornithochorous species have been focusing on various aspects of dispersal service, such as fruit removal, bird visitation rates to fruiting trees, and soil seed bank, bird-dispersed seed rain and seedling densities, both underneath and away from parent trees (e.g. Cordeiro & Howe 2003; Cramer et al. 2007; Herrera & Garcia 2010). In these studies, fragmentation was usually measured as a single parameter, either as a numerical gradient (i.e. from little to highly fragmented areas, e.g. Herrera & Garcia 2010) or as a categorical factor (i.e. isolated patches vs. continuous forest, e.g. Cordeiro & Howe 2003; Cramer et al. 2007). In a Tanzanian forest, Cordeiro & Howe (2003) found that isolated fragments had significantly lower densities and diversity of disperser birds, and seed removal rates on a fleshy-fruited species were over four times lower than in continuous forest. As a consequence, the percentages of "undispersed" conspecifics among all seedlings and juveniles present underneath parent tree crowns and at 10 m away from parent trees were much higher in isolated patches (respectively 91% and 36%) than in continuous forest (respectively 64% and 9%), whereas "dispersed" seeds were significantly less abundant in isolated patches, with only 19% of conspecific juveniles found 20 m away from parent trees, as opposed to the 61% found in continuous forest (Cordeiro & Howe 2003). Similarly, in a Brazilian forest, Cramer et al. (2007) found that a large-seeded tree had three times fewer seeds dispersed overall, and about fifty less seeds dispersed 10 m away from parent trees in isolated fragments than in continuous forest. Moreover, the five seeds deposited the furthest were found on average 25 m away from the parent tree crown in continuous forest, and only of 4 m on average in isolated fragments, regardless of fragment size (in 1 ha, 10 ha and 100 ha patches). However, the same study found no significant difference between continuous forest and isolated fragments in the amount and distance of dispersed seeds of a small-seeded tree species (Cramer et al. 2007). Herrera & Garcia (2010) used a fragmentation measure calculated as the amount of

tree canopy cover occupying large circular plots around central 50 cm x 50 cm quadrats, established to count the number of seeds dispersed by birds. They found a significant decrease in the number of bird-dispersed seeds along the forest fragmentation gradient, and observed that seed dispersal was mostly enhanced by the presence of woody perches and fleshy fruits in the vicinity, regardless of forest cover, suggesting a stronger influence of connectivity than forest area on dispersal service (Herrera & Garcia 2010).

Nevertheless, when looking at the individual effect of patch area, among four isolated fragments (located 4.9 to 7.9 km away from the continuous forest), seed removal rates were found to increase with patch area (from 2 to 31 ha), showing the lack of contribution to dispersal service of generalist birds of edge abounding in small fragments (Cordeiro & Howe 2003). In my study, *F. excorticata* fruit removal by birds was high in small fragments, where its guild of dispersers was also detected in significantly higher numbers than in large reserves.

V. Conclusion

In the native forest fragments of Banks Peninsula, local densities of frugivorous bird species had no significant effect on *F. excorticata* fruit consumption. Dispersal Index was significantly increasing with patch connectivity and with altitude. The implications for mutualistic interactions in a fragmented landscape are similar to that for bird densities: patch connectivity is of particular importance for the local removal of *F. excorticata* fruits, possibly leading to the provision of sufficient dispersal service. In contrast, patch area had no positive effect on seed dispersal, most likely because of the significantly higher abundance of frugivorous birds detected in small patches than in large reserves on Banks Peninsula (Chapter 2). These results are in line with that of various studies on seed dispersal by birds in fragmented forests, including Herrera & Garcia (2010) who suggest that "presence of scattered and remnant tree cover, and especially that providing fruit resources in unforested matrix, is the most important factor driving seed dispersal through the entire fragmented landscape". Therefore, allowing for a local increase in patch connectivity by supporting the regeneration of small native forest fragments and single fruiting trees scattered in the vicinity should result in improved dispersal service in sites lacking interactions with mutualist birds, and favour the deposition of seeds in regenerating patches, with positive outcome on gene flow throughout the network of thus better connected forest fragments.

The Dispersal Index developed by Robertson et al. (2008) is a practical tool to estimate local dispersal service in a single visit, however it should be used with particular attention to yearly and altitudinal variations in local ripening seasons, to avoid a possible overestimation of

results at both ends of the relative ripening season spectrum. Although *F. excorticata* trees of most sites in this study had apparently insufficient seed dispersal (over 40% of ripe fruits remaining undispersed by birds), the likelihood of local failure in dispersal service alone to result in local *F. excorticata* extinction is low, but may be more alarming at sites where both pollination and dispersal are failing.

CHAPTER 5:

Lowland forest fragmentation and inbreeding depression of *Fuchsia excorticata* on Banks Peninsula

Germination trial set up in the glasshouse, at the end of sowing day.

(Photo Marine Aubert)

I. Introduction

Since human settlement in New Zealand (by the end of the thirteenth century; Wilmshurst et al. 2008), over 77% of the originally extent native forest cover has been cleared and turned into mostly agricultural land (Ewers et al. 2006). Along with the severe effect of introduced mammal predators, habitat loss has contributed to the significant decline in native bird density and diversity, with 44% of native forest bird species being now range-restricted (Holdaway 1989; Holdaway 1999; Innes et al. 2010; Tennyson 2010). Several native bird species have been identified as important pollinators for animal-pollinated native plants (Anderson 2003; Kelly et al. 2006; Anderson et al. 2016), and the decrease in richness and abundance of pollinator birds has been associated with growing evidence of local disruptions in plant-pollinator interactions, with detrimental effects on the regeneration of various native plant species (Kaiser-Bunbury et al. 2010; Kelly et al. 2006; Iles & Kelly 2014). Low densities of pollinators may result in insufficient pollination service, through the deposition of limited pollen quantity or poor pollen quality, including consideration of self-incompatibility and inbreeding depression (Wilcock & Neiland 2002). For plants relying on animals for pollination, the negative impact of pollinator decline on offspring abundance has been well demonstrated (Quesada et al. 2004), whereas the effects on progeny quality have been little studied. Recent findings seemed to indicate that pollinator limitation can have a positive effect on seedling fitness, as low pollinator densities were associated with low seed set but high outcrossing rates through intraspecific competition for pollinator services (Delmas et al. 2015).

In the absence of interaction with mutualist pollinators, reproductive assurance in self-compatible flowering plants allows for the production of seeds from self-pollination (Darwin 1876; Baker 1955; Baker 1967). When the seeds resulting from selfing have the fitness to germinate, grow and survive to a fertile adult stage, self-compatibility represents a valuable survival mechanism that can compensate for poor pollination service. This reproductive strategy can ensure successful plant reproduction when conditions are detrimental to mutualistic interactions, e.g. after the recent establishment of a long-distance colonists that hasn't yet formed mutualist partnerships with the local guild of pollinators, especially on islands where an important proportion of the local flora has established through long-distance dispersal and is thus likely to be fully or partially self-compatible (Darwin 1876; Baker 1955; Baker 1967; Lloyd & Schoen 1992; Fausto et al. 2001; Schueller 2004; Moeller & Geber 2005). However, the fitness of seeds produced via self-pollination is often low because of inbreeding depression, manifested by poor germination success, failure to survive to a mature stage or inability to produce seeds as an adult (Darwin 1876; Charlesworth & Charlesworth 1987). Thus,

selfed and crossed individuals have been commonly found to co-occur among seeds of self-compatible species, but not among adults, as strong inbreeding depression prevented lasting survival and maturing of selfed seedlings (Hardner & Potts 1997; Goodwillie et al. 2005). In the long term, recurrently high selfing rates caused by a lack of pollinators can result in severe decrease in genetic diversity and reduced gene flow (Stebbins 1957). Long-lived and large-statured plants are particularly affected by inbreeding depression, resulting in the total failure of selfed offspring to reach a mature stage (Scofield & Schultz 2006). In bird-pollinated trees, important inbreeding depression may thus prevent the reproductive assurance of self-compatibility (Robertson et al. 2011; Van Etten et al. 2015). As pollination by birds has been associated globally with high outcrossing rates, in comparison to insects that tend to move between flowers of single plants resulting in self-pollination through geitonogamy, the lack of interaction with pollinator birds is of particular concern for the persistence of self-compatible trees in New Zealand (Anderson et al. 2016).

Habitat fragmentation is known to decrease the density and diversity of species from the original biota, and to reduce the mobility of individuals, including pollinators, between remnant patches as the distance between them increases (Andren 1994; Kearns et al. 1998). The patterns of gene flow and inbreeding depression may thus be affected through modifications in the quantity and quality of pollen being dispersed by pollinators between and within plant populations (Harris & Johnson 2004; Sork & Smouse 2006; Lander et al. 2010). Inbreeding depression caused by gene flow limitation or genetic isolation can lead to genetic loss and divergence between disconnected populations (Dick et al. 2003; Sork & Smouse 2006). Because of the conspicuousness of flower displays in large plant populations, pollinators are more likely to be attracted to large remnant patches; small and isolated populations may thus be at particular risk of extinction, as population size has been negatively linked with disruption in pollen flow, increased mating with close relatives, and inbreeding depression (Byrne et al. 2007; Coates et al. 2007). However, fragmentation does not necessarily result in genetic isolation, as pollen movements between forest patches have been shown to be maintained and sometimes even increased between sites, including small patches and single standing trees (Dick et al. 2003; Sork & Smouse 2006; Byrne et al. 2007; Lander et al. 2010). Within a vegetation fragment, the foraging behaviour of pollinators is also affected by local plant species density, with flower visitation and outcrossing rates increasing with decreasing distance between flowering individuals, whereas sparse populations are more likely to experience limited pollen transfer between plants and higher frequencies of pollination within single plants (Mustajarvi et al. 2001).

Fuchsia excorticata is a bird-pollinated tree that has been shown to suffer pollen limitation at low pollinator densities (Robertson et al. 2008). In order to assess the severity of inbreeding depression in *F. excorticata*, a field comparison of the percentage of selfed individuals at various growth stages (seed set, germination, establishment, growth and survival rates) allowed Robertson et al. (2011) to demonstrate the low fitness of self-pollinated seeds in the self-compatible hermaphrodites. There was no significant difference in seed set between fruits produced by self- and cross-pollination (Robertson et al. 2008), but germination rate measured as the percentage of germinated seeds was lower in self-pollinated hermaphrodites than in outcrossed seeds from female or hermaphrodite parents, by 14% and 39% respectively from two source populations (Robertson et al. 2011). Growth and survival rates were particularly poor in selfed seedlings in comparison to crossed individuals, providing evidence of the high inbreeding depression of self-compatible hermaphrodites revealed in late plant development stages despite being hardly detectable at the seed or germination stages (Robertson et al. 2011). This cryptic recruitment failure occurring in the absence of sufficient interaction with pollinator birds may threaten the local persistence of *F. excorticata* populations in native forest fragments.

In this chapter, I aimed to identify which fragmentation parameters were affecting inbreeding depression in *Fuchsia excorticata*. I measured inbreeding depression by comparing the seed set, germination and growth rates of female and hermaphrodite offspring. Are the factors affecting inbreeding depression similar to those affecting pollination service or bird densities? What site characteristics are associated with high inbreeding depression and increased local extinction risk?

II. Methods

Seed set

Fuchsia excorticata fruits are approximately 12 × 5 mm berries, divided into four locules, containing c. 300–600 small seeds in total (Godley & Berry 1995). A possible consequence of poor pollination service is a decrease in seed production: low quantity or poor quality of pollen deposition on the flower's stigma may lead to the production of fewer seeds per fruit. *F. excorticata* berries typically contain two types of seeds: "unfilled" seeds (germination < 1%) are flat and translucent, while "filled" seeds (germination > 80%) are fat and dark (Robertson et al. 2008). The unfilled seeds are thought to be largely non-pollinated (Robertson et al. 2008).

Therefore, I chose to ignore unfilled seeds and take only filled seeds into account in order to analyse seed set data and compare with pollination results from Chapter 3.

In a study comparing pollination treatments of *F. excorticata* flowers (none, natural, and hand crossed pollination on both sexes, and hand self-pollination on hermaphrodites only) Robertson et al. (2008) found that bagged (not pollinated) female flowers didn't ripen any fruit, but that once a fruit was formed, there was no significant effect of pollination treatment on the total number of filled seeds per fruit. The similarity in seed set between self- and cross-pollinated fruits, and between females and hermaphrodites, seemed to indicate that pollen quantity rather than quality may be the main determinant of seed production per fruit.

In summer 2013-14, I collected ripe *F. excorticata* fruits in 11 lowland forest fragments on Banks Peninsula, from 4 to 11 trees per site (Table 5.1). Fruits were sampled from trees of known sex, so that the local difference between seed sets per fruit on females and hermaphrodites could be assessed. I aimed to collect 10 fruits per tree. Because of the reduced availability in accessible fruits in some cases, there was a total of 871 fruits from 92 trees, including 10 fruits per tree from 71 trees, and 21 trees with more or fewer fruits collected (Table 5.1). The berries were dissected under a microscope and filled seeds were counted in one of the four locules per fruit. Some of the seed counts were carried out by a field assistant under my supervision. The total number of seeds per fruit was thus about four times the number of seeds counted per locule, and I used the number of seeds per locule as an estimate of seed set.

Table 5.1: Number of *Fuchsia excorticata* fruits sampled per tree during summer 2013-14 from 92 trees in 11 lowland forest fragments on Banks Peninsula.

N. of fruits collected	20	11	10	9	8	7	6	4	3	2
N. of trees sampled	2	1	71	4	2	2	4	3	2	1

Germination rate and seedling growth performance

In plants able to self-pollinate, inbreeding depression under natural or semi-natural conditions can be tested by the reproductive outcome of selfing by assessing the fitness of selfed offspring. As inbreeding depression can reveal itself at any life-stage, offspring placed under the influence of similar biotic and abiotic factors could be surveyed over an extended period of time, from germination to plant establishment.

Hermaphrodite *F. excorticata* flowers are able to self-pollinate, while female flowers are necessarily cross-pollinated through the external input of pollen from hermaphrodite flowers. Cross-pollinated offspring of females and hermaphrodites are expected to have similar fitness

levels, whereas self-pollinated offspring may not be as fit if affected by inbreeding depression. Therefore, significant differences in seeds and seedlings performance between the offspring of females and hermaphrodites may indicate high levels of self-pollination in hermaphrodites. In their 11-year assessment of inbreeding depression in two *F. excorticata* populations, Robertson et al. (2011) found that seeds from self-pollinated flowers had significantly lower germination rates, lower survival rates, and lower mean stem heights in pots, than seeds from cross-pollinated hermaphrodite and female flowers, which had equivalent numbers. Site-specific low germination rates and slow growth of progeny may suggest locally poor gene flow, indicative of a limited genetic pool, reduced pollination service, and high inbreeding depression.

In a glasshouse experiment, I estimated the prevalence of inbreeding depression in *Fuchsia excorticata* by comparing the germination rates and growth performances of naturally pollinated progeny from females (all outcrossed) and hermaphrodites (unknown mix of selfed and crossed) from 11 *Fuchsia excorticata* populations. In summer 2013-14, 5 to 35 seeds per fruit were randomly extracted from the ripe *F. excorticata* berries collected in 11 sites on 93 trees (the 92 trees used to count seeds per locule, plus one hermaphrodite tree in Oashore which had not been counted, but its seeds were sown in the germination trial). The berries were collected on both hermaphrodite and female trees at all sites except in Oashore where no fruiting female was found. All seeds from the same known parent, i.e. extracted from berries sampled on the same mother plant, were combined into one seed-pool per parent tree, so random variation among fruits per tree would not affect the results. Each seed-pool was then divided into five equal portions of 5 to 35 seeds, sown in five labelled pots in August 2014 (with the help of a field assistant), and set up in the glasshouse for a germination trial. In order to control for differences in environmental conditions in the glasshouse, the pots were shifted around regularly. The total number of seedlings present in each pot was counted regularly by a field assistant. Germination rates were calculated per mother tree as the final percentage of total seeds that had germinated in the 5 pots by November 2014 (three months after sowing), out of the total number of seeds sown in these pots, to avoid having nested levels of replication (trees within reserves and pots within trees). The heights of 6 random seedlings were recorded in each pot in January 2015 (five months after sowing) for 88 trees by field assistants, who mistakenly omitted the pots from 5 parent trees (one from Montgomery and four from Otepatotu). The minimum, maximum and average heights of seedling per pot were determined five months after sowing, and the mean value of each measurement was calculated by averaging the five pots per mother tree (again to avoid nested replication).

Site-specific parameters: biotic and abiotic factors

A lack of interaction with mutualist birds can lead hermaphrodite *F. excorticata* trees to self-pollinate, and cross-pollination on females and hermaphrodites to occur between close relatives. Therefore, site specific factors influencing pollination service in forest fragments were expected to have similar effects on inbreeding depression. On Banks Peninsula, *F. excorticata*'s main flower visitors were bellbird and silvereye, which both tended to decrease with area and to increase with patch connectivity (landscape-scale connectivity index dH). In Chapter 3, pollination service to female flowers was found to improve with area in sites smaller than 15 ha, but was found to decrease again in larger sites. Pollination success was also higher in sites with low *F. excorticata* densities, and slightly affected by a negative edge effect. The variables that were found to affect pollination in Chapter 3 were expected to have a similar effect on inbreeding depression. Therefore, to determine which factors were significant predictors of *F. excorticata*'s seed set quality and inbreeding depression levels, I tested all the site variables used in earlier chapters. For each study site where seeds were collected, the number of trees sampled, site-specific parameters, and flower visitor bird densities are presented in Table 5.2.

Table 5.2: Number (n) of fruiting *Fuchsia excorticata* trees sampled during summer 2013-14, altitude, area, dH and ADRA value, importance of *F. excorticata* in the forest canopy, and average number of flower visitor birds (bellbird and silvereye) detected per 5-min count (data 2005-16) in 11 lowland forest fragments on Banks Peninsula.

Site	n	Alt. (m)	Area (ha)	ADRA ($ha.m^{-1}$)	dH (%)	*F. exc.* density	Bellbirds / 5min	Silvereyes / 5 min
CloudFarm	10	620	4.05	1.60	1.88	3	2.65	2.65
Hay	4	35	6.37	0.12	0.95	1	3.32	1.21
Hinewai	10	400	93.44	7.48	4.39	3	2.31	0.88
MagnetBay	10	240	29.49	0.77	1.21	2	2.65	1.12
Montgomery	10	500	23.38	0.13	0.50	3	2.83	2.29
MtPearce	9	540	38.07	3.77	1.32	3	0.88	0.47
Oashore	6	240	12.87	0.03	1.08	1	2.53	2.56
Otepatotu	8	660	16.84	2.30	1.00	3	1.81	0.75
TipperaryGully	5	300	2.84	0.01	0.09	1	0.35	2.41
Tutakakahikura	10	380	12.89	2.57	0.44	2	2.09	1.91
Whatarangi	11	580	5.22	0.43	1.27	3	2.65	2.12

Statistical analyses

All statistical analyses were performed using the program R version 3.1.1 (R Core Team 2014). Seed set per fruit was expressed as the number of filled seeds per locule. The average

seed set per *F. excorticata* tree was calculated for the 92 trees using a total of 871 fruits. Plant mean seeds per locule were normally distributed.

Similarly, germination rates were calculated for 93 trees by dividing the total number of seeds sown per mother tree by the number of seeds that germinated by three months after sowing within all 5 pots from the same mother, in order to remove the random effect of pot per tree. I used a binomial GLM on germination data using the *cbind* command, which combined the number of germinated and ungerminated seeds for each tree, while allowing for data structure by taking into account the variation between samples in total number of seeds sown per pot (mean seeds per pot = 20.5, range 5 to 35). The analyses testing the effect of various factors on inbreeding depression were performed using the average germination rate per mother tree, calculated for 93 parent trees, and the minimum, maximum and mean seedling height per mother tree at 5 months after sowing, calculated for 88 parent trees.

I tested the effects of sex and site on seeds per locule, germination rate, minimum, maximum and mean seedling height using generalized linear models and found a significant effect of site on each of these variables (Table 5.3).

- *Seed set*

To identify which site-specific parameters may explain this variation on *F. excorticata* seed set, I used the raw dataset of 871 seed counts per locule to run ten single-factor generalized linear mixed models (GLMM) with Poisson error distribution (*lme4* package in R), allowing for data structure by including a random term for tree within site, and analysed with an ANOVA based on Chi-squared test (*Anova* command from *car* package in R).

I used the formula: *glmer(Seeds ~ x + (1|Site/TreeID), family = poisson)*, where the explanatory variable x was respectively altitude, area, connectivity indices dH and ADRA, edge, *F. excorticata* density, mean number of bellbird, and mean number of silvereye detected per count. Area, dH and ADRA were log-transformed in order to increase the normality of their distribution across data. The model was run separately on each sex, because there was a significant difference between female and hermaphrodite trees in the number of seeds per locule.

In Chapter 3, the fluctuation in pollination service between sites on female *F. excorticata* flowers was significantly correlated with a quadratic effect of log(Area), and a comparable effect was observed on female seed set data, with an initial increase in mean number of filled seed per locule followed by a plateau in larger sites (Figure 5.1). Therefore, the term log(Area) was replaced by poly(log(Area),2) in the GLMM.

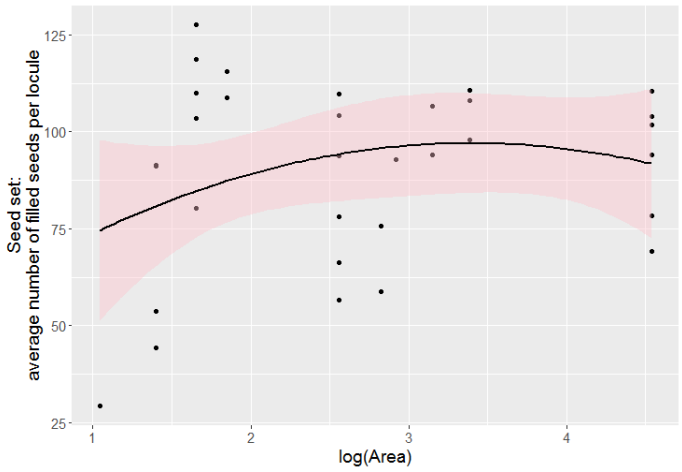

Figure 5.1: Scatter plot of mean seed set per female *Fuchsia excorticata* tree against log(Area) with fitted quadratic regression line.

All parameters with an individual effect significant at $p < 0.1$ and a $\Delta AIC < 5$ between these single-factor models were then included in a model selection process, starting with a new GLMM with Poisson error distribution and similar random terms to those in the single-factor GLMMs, then manually removing fixed-effect parameters one at a time (*drop1* command in R, with *test = « Chisq »*). This stepwise backward model selection was repeated until no parameter elimination would decrease further the model's AIC. The final model best explaining the data was then analyzed with an ANOVA based on Chi-squared test.

- *Germination rate*

Similarly, I ran ten single-factor GLMMs with binomial error distribution, testing the effect of the same parameters on the raw dataset of 465 germination rates per pot (5 pots per mother tree), allowing for the nested structure of the data by including a random term for pot within tree within site, and analysed with an ANOVA based on Chi-squared test.

I used the formula: *glmer(GermRate ~ x + (1|Site/TreeID/pot), family = binomial)*, where the explanatory variable x was respectively altitude, area, connectivity indices dH and ADRA, edge, *F. excorticata* density, mean number of bellbird, and mean number of silvereye detected per count. Area, dH and ADRA were log-transformed in order to increase the normality of their distribution across data. The model was run on both sexes combined for germination rates, as the effect of parent sex was non-significant (Table 5.3).

All parameters with an individual effect significant at $p < 0.1$ and a $\Delta AIC < 5$ between these single-factor models were then included in a model selection process, starting with a new GLMM with binomial error distribution and similar random terms to those in the single-factor GLMMs, then manually removing fixed-effect parameters one at a time (*drop1* command in R, with *test = « Chisq »*). This stepwise backward model selection was repeated until no parameter elimination would decrease further the model's AIC. The final model best explaining the data was then analyzed with an ANOVA based on Chi-squared test.

- *Seedling growth*

In order to detect local inbreeding depression among hermaphrodites' progeny, despite the higher variation between sites in mean seedling height than between sexes of parent trees (Table 5.3), I also ran an analysis using a measure that was neither impacted by resource competition in the glasshouse, nor by local phenotypes: the local growth performance of hermaphrodites' offspring, calculated as the difference Hdiff in average mean seedling height per mother tree between hermaphrodites' (Hh) and females' (Hf) progeny: Hdiff = Hh - Hf. The dataset of local height difference had only one value per site in eight sites, so it was not suited for analysis in a complex multi-factor model. The effects of each site-specific parameters and mean number of pollinator birds per count at each site on Ds were tested individually using Gaussian generalized linear models, using the formula: *glm(formula = Hdiff ~ x)* with the explanatory factor x being respectively altitude, log(Area), log(dH), log(ADRA), *F. excorticata* density, edge, and bellbird + silvereye.

III. Results

Seed set measured as the mean number of seeds per locule in a fruit, germination rate estimated as the final percentage of seeds that had germinated 3 months after sowing, and minimum, maximum and mean seedling height measured 5 months after sowing, were all significantly affected by site (Table 5.3). The difference between offspring of hermaphrodites and females was only detected among all sites for the number of seeds per locule, as a result of the difference in pollen quantity deposited on flowers of each sex, and for the mean seedling height (Table 5.3). There was no difference between sexes in minimum and maximum seedling heights

per mother tree, and the high variation between sites in mean seedling height was also more important than the variation between seedlings of each sex (Table 5.3).

Table 5.3: Analysis of deviance table from the GLMs assessing the effect of sex and site on seeds per locule, germination rate, minimum, maximum and mean seedling height of *Fuchsia excorticata* trees. Bold p-values indicate a significant effect ($p < 0.05$).

Response variable	Parameter	Df	Deviance	Resid. Df	Resid. Dev	p(>F)
Seeds per locule	NULL			91	34977	
	Sex	1	1367.3	90	33610	**0.009**
	Site	10	14186.3	80	19424	**< 0.001**
	Sex:Site	9	5195.1	71	14229	**0.002**
Germination rate	NULL			92	1393.63	
	Sex	1	0.01	91	1393.62	0.977
	Site	10	487.57	81	906.05	**< 0.001**
	Sex:Site	9	109.36	72	796.68	0.307
Min. seedling height	NULL			87	198433	
	Sex	1	1228	86	197205	0.382
	Site	10	84366	76	112840	**< 0.001**
	Sex:Site	8	5178	68	107662	0.912
Max. seedling height	NULL			87	357036	
	Sex	1	30	86	357005	0.909
	Site	10	191411	76	165594	**< 0.001**
	Sex:Site	8	7582	68	158012	0.912
Mean. seedling height	NULL			87	306426	
	Sex	1	8741	86	297685	**0.009**
	Site	10	214166	76	83518	**< 0.001**
	Sex:Site	8	2343	68	81175	0.980

Seed set

As the number of filled seeds has been associated with the quantity rather than the quality of pollen deposition on *F. excorticata* flowers, seed set in fruits of female trees were expected to be lower than on hermaphrodites in sites with evidence of poor pollination service. Similarly, as self-pollination mechanisms lead pollen scores to be always high on hermaphrodite *F. excorticata* flowers, and seed set in a fruit is a direct reflection of pollen quantity deposited onto flower stigma, no significant effects of site parameters were expected on seed set of hermaphrodites.

The results showed that the difference in seeds per locule between sexes were as anticipated: the number of seeds per locule on hermaphrodite trees was significantly higher than seeds per locule on females across all sites, and the effect of sex within site was also significant, with a high variation between sites (Table 5.3, Figure 5.2). However, no correlation

was found between mean seeds per locule per site on females and mean female pollen load score per site (R^2 = 0.0076, p = 0.811).

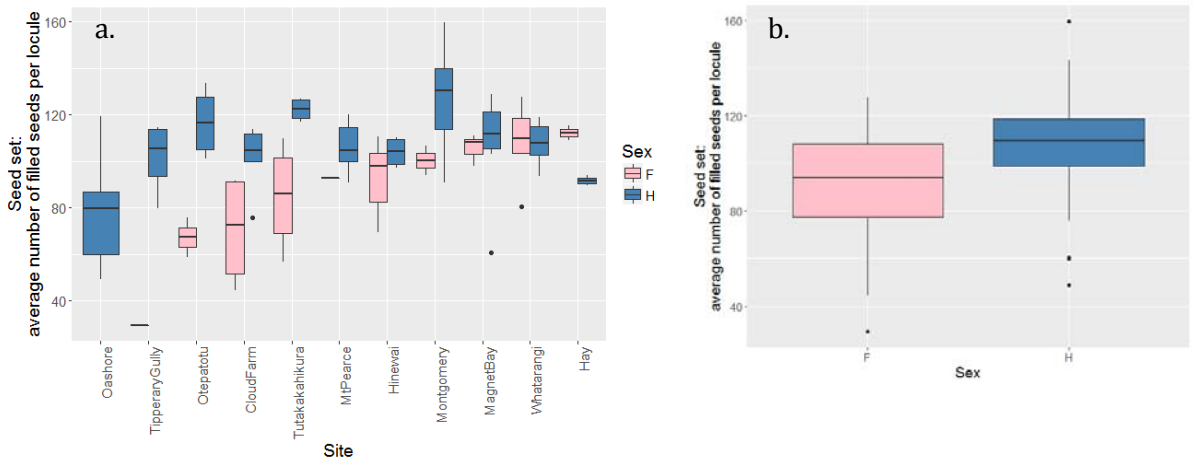

Figure 5.2: Boxplots of mean seeds per locule per tree on female and hermaphrodite *Fuchsia excorticata* in 11 lowland forest fragments on Banks Peninsula, (a) ordered per site by increasing values on females, and (b) sorted per parent sex across all sites.

In female fruits, the model identified a significant (p < 0.1) effect of area, dH and Bellbird on the number of seeds per locule (Table 5.4).

In hermaphrodite fruits, there was a significant (p<0.1) effect of altitude, edge and *F. excorticata* density on the number of seeds per locule (Table 5.4).

Table 5.4: Analysis of variance table from the ANOVAs, with coefficients and standard errors from summary output of the generalized linear mixed models assessing the effects of altitude, area, dH, ADRA, edge, *F. excorticata* density, bellbird and silvereye densities on the number of seeds per locule in female and hermaphrodite *Fuchsia excorticata* fruits. Bold p-values indicate a significant effect ($p < 0.1$).

Response var.	Parameter	Coef.	Std. error	Df	Chisq.	p(>Chisq)	AIC
Seeds per locule in female fruits	Intercept	4.5405	0.2468				
	Altitude	-0.2817	0.5251	1	0.2878	0.5917	4517.5
	Intercept	4.4305	0.0843				
	Poly(log(Area),1)	1.5627	1.5423				
	Poly(log(Area),2)	-2.1781	1.3748	2	5.0378	**0.0805**	**4514.9**
	Intercept	4.4269	0.0849				
	log(dH)	0.2080	0.0961	1	4.6866	**0.0304**	**4513.1**
	Intercept	4.4389	0.0969				
	log(ADRA)	0.0720	0.0549	1	1.7157	0.1902	4516.0
	Intercept	4.3548	0.1081				
	Edge	0.1028	0.0749	1	1.8821	0.1701	4515.9
	Intercept (low)	4.1407	0.2340				
	FEdensity (med.)	0.3883	0.3076				
	FEdensity (high)	0.3158	0.2629	2	1.813	0.4039	4517.9
	Intercept	4.0117	0.2293				
	Bellbird	0.1984	0.1017	1	3.802	**0.0512**	**4514.2**
	Intercept	4.6710	0.2254				
	Silvereye	-0.1564	0.1296	1	1.4556	0.2276	4516.4
Seeds per locule in hermaphrodite fruits	Intercept	4.4896	0.0919				
	Altitude	0.3816	0.1978	1	3.7211	**0.0537**	**7615.8**
	Intercept	4.5832	0.1084				
	log(Area)	0.0263	0.0384	1	0.4701	0.493	7618.6
	Intercept	4.6508	0.0385				
	log(dH)	-0.0237	0.0421	1	0.3158	0.5741	7618.7
	Intercept	4.6706	0.0378				
	log(ADRA)	0.0275	0.0182	1	2.2755	**0.1314**	**7616.9**
	Intercept	4.5965	0.0458				
	Edge	0.0574	0.0252	1	5.2029	**0.0225**	**7614.1**
	Intercept (low)	4.4743	0.0605				
	FEdensity (med.)	0.2428	0.0872				
	FEdensity (high)	0.2265	0.0699	2	11.621	**0.0029**	**7612.8**
	Intercept	4.6692	0.0968				
	Bellbird	-0.0084	0.0447	1	0.0355	0.8505	7619
	Intercept	4.7107	0.0904				
	Silvereye	-0.0346	0.0490	1	0.4992	0.4798	7618.6

On female seed set, the initial GLMM included three significant ($p<0.1$) parameters: area, connectivity index dH, and bellbird density. I ran the stepwise backward analysis the formula *glmer(Seeds ~ poly(log(Area),2) + log(dH) + Bellbird + (1|Site/TreeID), family = "poisson")* and none of these parameters were dropped by the model selection. The output of this final model is presented in Table 5.5.

Table 5.5: Summary output of the selected GLMM testing the effect of area, dH and bellbird density, on the number of seeds per locule in female *F. excorticata* fruits in 10 lowland forest sites on Banks Peninsula, taking into account the random effects of parent trees within sites. Bold p-values indicate a significant effect ($p < 0.05$).

Generalized linear mixed model fit by maximum likelihood

Family	poisson (log)				
Formula	*Seeds ~ poly(log(Area), 2) + log(dH) + Bellbird + (1 | Site/TreeID)*				
Information criteria	AIC	BIC	logLik	deviance	df. residuals
	4510.0	4535.4	-2248.0	4496.0	273
Scaled residuals	Min	1Q	Median	3Q	Max
	-7.5572	-1.5816	0.1581	1.8469	10.5768
Random effects	Groups	Name	Variance	Std. Dev.	Number of obs.
	TreeID:Site	(Intercept)	0.0465	.2156	32
	Site	(Intercept)	0.0122	0.1103	10
					280
Fixed effects		Estimate	Std. Error	z value	p(>|z|)
	(Intercept)	4.1357	0.1793	23.065	<0.001
	poly(log(Area), 2)1	0.2659	1.3726	0.194	0.8463
	poly(log(Area), 2)2	-2.7706	1.0175	-2.723	**0.0065**
	log(dH)	0.1630	0.0920	1.772	**0.0765**
	Bellbird	0.1379	0.0828	1.665	**0.0959**
Correlation of Fixed Effects		(Intercept)	poly(log(A))1	poly(log(A))2	Log(dH)
	poly(log(Area), 2)1	-0.395			
	poly(log(Area), 2)2	-0.146	0.464		
	log(dH)	0.434	-0.691	-0.478	
	Bellbird	-0.950	0.472	0.195	-0.509

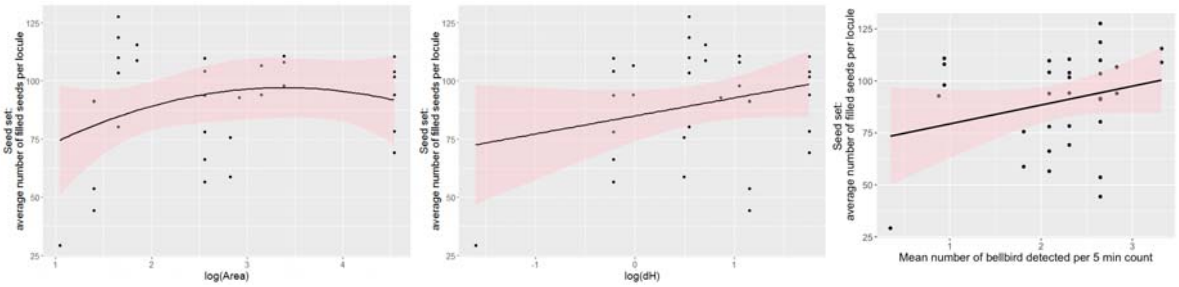

Figure 5.3: scatter plots with fitted regression lines of parameters kept by the model selection on the average number of filled seeds per locule in female *F. excorticata* fruits (mean per mother tree): (a) log(Area), (b) log(dH), and (c) mean number of bellbird detected per count.

On hermaphrodite data, the initial GLMM included the three significant ($p<0.1$) parameters: altitude, edge and *F. excorticata* density. I used the formula: *glmer(Seeds ~ Altitude + Edge + as.factor(FEdensity) + (1|Site/TreeID), control = glmerControl(optimizer = "bobyqa"), family = "poisson")*, including a control command to help the model converge. The model selection

suggested dropping altitude, but keeping edge and *F. excorticata* density in the final model (Table 5.6).

Table 5.6: Summary output of the selected GLMM testing the effect of edge and *F. excorticata* density on the number of seeds per locule in hermaphrodite *F. excorticata* fruits in 11 lowland forest sites on Banks Peninsula, taking into account the random effects of parent trees within sites. Bold p-values indicate a significant effect ($p < 0.05$).

Generalized linear mixed model fit by maximum likelihood

Family	poisson (log)				
Formula	*Seeds ~ Edge + as.factor(FEdensity)+ (1 | Site/TreeID)*				
Information criteria	AIC	BIC	logLik	deviance	df. residuals
	7610.7	7637.0	-3799.3	7598.7	585
Scaled residuals	Min	1Q	Median	3Q	Max
	-8.1827	-1.1649	0.1985	1.4610	7.1487
Random effects	Groups	Name	Variance	Std. Dev.	Number of obs.
	TreeID:Site	(Intercept)	0.0251	0.1585	60
	Site	(Intercept)	0.0034	0.0582	11
					591
Fixed effects		Estimate	Std. Error	z value	p(>|z|)
	(Intercept)	4.4336	0.0643	68.99	<0.001
	Edge	0.0518	0.0249	2.08	**0.0378**
	as.factor(FEdensity)2	0.2379	0.0885	2.69	**0.0072**
	as.factor(FEdensity)3	0.2126	0.0711	2.99	**0.0028**
Correlation of Fixed Effects		(Intercept)	Edge	as.f(FEd)2	
	Edge	-0.313			
	as.factor(FEdensity)2	-0.642	-0.026		
	as.factor(FEdensity)3	-0.791	-0.086	0.589	

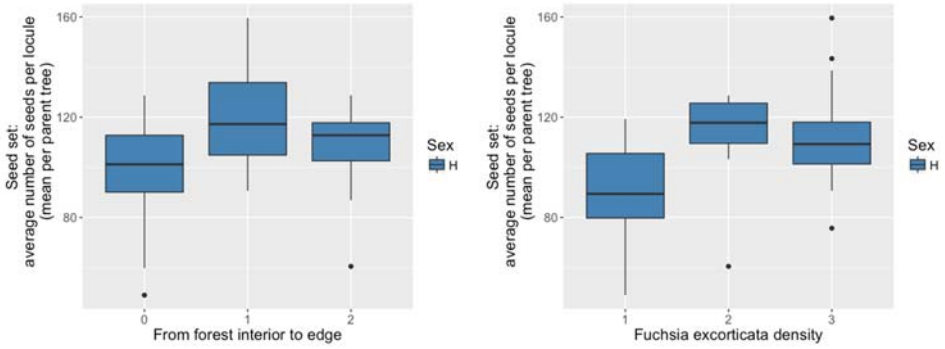

Figure 5.4: boxplot of parameters kept by the model selection on the average number of filled seeds per locule in hermaphrodite *F. excorticata* fruits (mean per mother tree): (a) edge, and (b) *F. excorticata* density.

Germination rates

There was no significant difference in germination rate between female and hermaphrodite's offspring across all sites and within sites (Table 5.3, Figure 5.4) so the models were run on all germination data from offspring of both female and hermaphrodite trees.

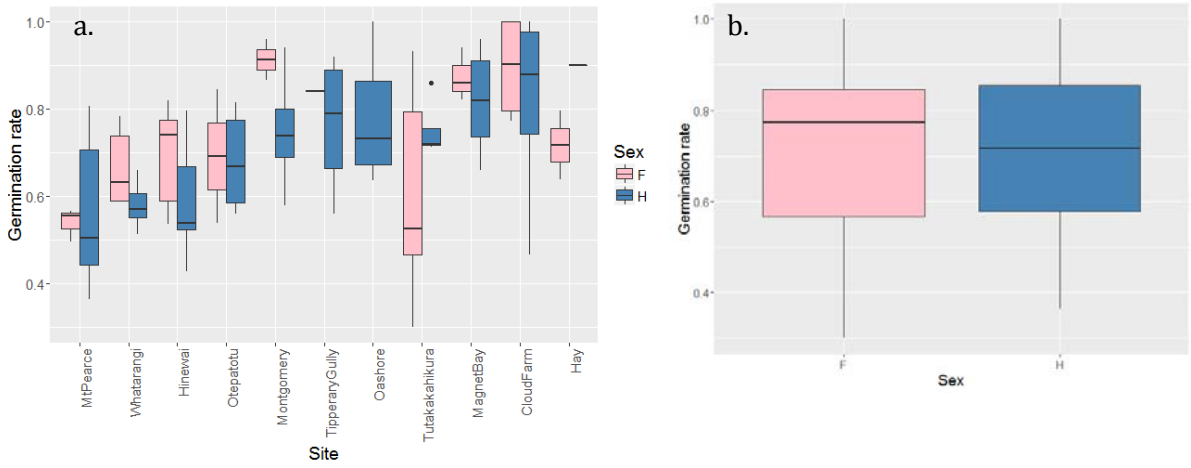

Figure 5.4: Boxplots of average germination rate per parent tree on female and hermaphrodite *Fuchsia excorticata* in 11 lowland forest fragments on Banks Peninsula, (a) ordered per site by increasing values on hermaphrodites, and (b) sorted per parent sex across all sites.

None of the parameters tested had a significant effect ($p<0.1$) on germination rate of *F. excorticata* seeds, but the effect of bellbird had a p-value equal to the significance limit for inclusion in the model selection ($p=0.1$, Table 5.7), and the next two predictors all had low dAIC values compared to bellbird. Therefore, a stepwise backard analysis was performed on the GLMM including three predictors : edge, bellbird and silvereye density as the fixed effect terms, using the formula : *glmer(GRate ~ Edge + Bellbird + Silvereye + (1|Site/TreeID), family = "binomial").* The model selection suggested dropping silvereye density and edge, but keeping bellbird density in the final model (Table 5.8, Figure 5.5).

Table 5.7: Analysis of variance table from the ANOVAs, with coefficients and standard errors from summary output of the generalized linear mixed models assessing the effects of altitude, area, dH, ADRA, edge, *F. excorticata* density, bellbird and silvereye densities on the proportion of *Fuchsia excorticata* seeds germinated per pot. Bold p-values indicate a significant effect ($p < 0.1$).

Response var.	Parameter	Coef.	Std. error	Df	Chisq.	p(>Chisq)	AIC
Germination rate	Intercept	1.3800	0.5254				
	Altitude	-0.6019	1.1507	1	0.2736	0.6009	2410.7
	Intercept	1.4362	0.5649				
	log(Area)	-0.1173	0.1998	1	0.3445	0.5572	2410.6
	Intercept	1.1367	0.2039				
	log(dH)	0.1459	0.2198	1	0.4407	0.5068	2410.5
	Intercept	1.1357	0.2150				
	log(ADRA)	0.0147	0.1032	1	0.0202	0.8869	2410.9
	Intercept	1.2500	0.2213				
	Edge	-0.1479	0.1116	1	1.7556	0.1852	**2409.2**
	Intercept (low)	1.0213	0.3965				
	FEdensity (med.)	0.5945	0.5932				
	FEdensity (high)	-0.0145	0.4701	2	1.5228	0.4670	2411.5
	Intercept	0.4096	0.4734				
	Bellbird	0.3547	0.2156	1	2.7053	**0.1000**	**2408.5**
	Intercept	0.5877	0.4538				
	Silvereye	0.3240	0.2483	1	1.7023	0.1920	**2409.4**

Table 5.8: Summary output of the selected GLMM testing the effect of bellbird density on the number of *F. excorticata* seeds germinated per pot from 11 lowland forest sites on Banks Peninsula, taking into account the random effects of parent trees within sites. Bold p-values indicate a significant effect ($p<0.05$).

Generalized linear mixed model fit by maximum likelihood

Family	binomial (logit)				
Formula	*GermRate ~ Bellbird + (1 | Site/TreeID)*				
Information criteria	AIC	BIC	logLik	deviance	df. residuals
	2408.5	2425.0	-1200.2	2400.5	461
Scaled residuals	Min	1Q	Median	3Q	Max
	-5.7032	-0.6999	0.1529	0.8752	4.6061
Random effects	Groups	Name	Variance	Std. Dev.	Number of obs.
	TreeID:Site	(Intercept)	0.6790	0.8240	93
	Site	(Intercept)	0.2842	0.5331	11
					465
Fixed effects		Estimate	Std. Error	z value	p(>|z|)
	(Intercept)	0.4096	0.4734	0.865	0.387
	Bellbird	0.3547	0.2156	1.645	0.100
Correlation of Fixed Effects		(Intercept)			
	Bellbird	-0.918			

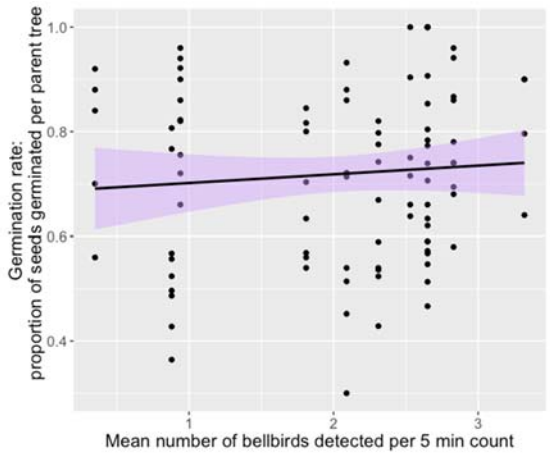

Figure 5.5: scatter plot with fitted regression line of the only parameter kept by the model selection: the mean number of bellbirds detected per count on the average number of *F. excorticata* seeds germinated per pot, from 11 lowland forest sites on Banks Peninsula.

Seedling growth performance

There was no difference between sexes of parent tree in minimum and maximum seedling heights per pot, but a significant effect of site (Table 5.3). There was a significant difference between parent sexes in mean seedling height per parent tree (Table 5.3), with seedlings of female parents generally taller than seedlings of hermaphrodites, but this difference was overpowered by the variation between sites (Figure 5.6).

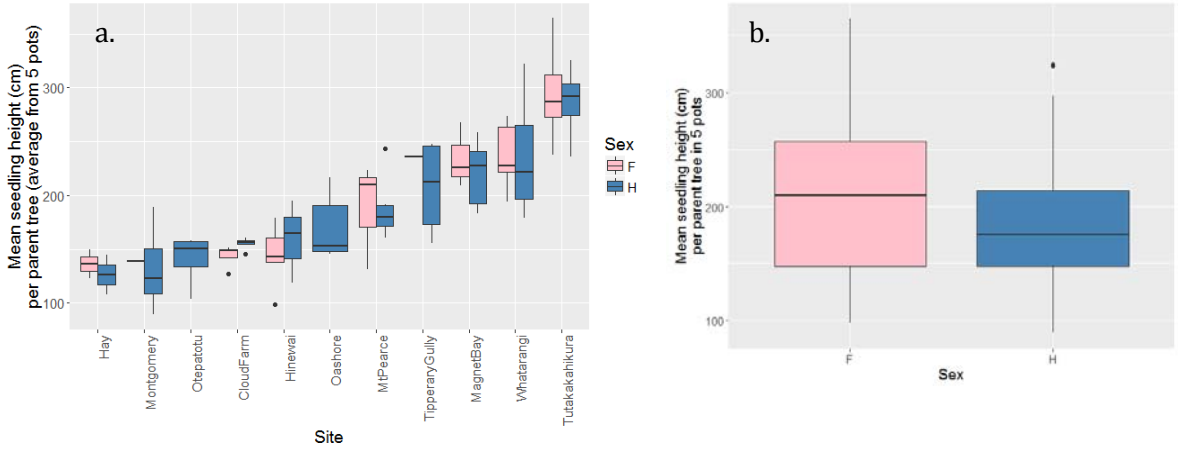

Figure 5.6: Boxplots of average seedling height per parent tree in offspring of female and hermaphrodite *Fuchsia excorticata* trees in 11 lowland forest fragments on Banks Peninsula, (a) ordered per site by increasing height of hermaphrodite seedlings, and (b) sorted per parent sex across all sites.

As female trees are always cross-pollinated, their offspring would be expected to grow at similar rates regardless of the source population. The absence of significant variation between sexes of parent trees within sites (non-significant Sex:Site interaction, Table 5.3) may be an indication that differences between sites in growth rate of seedlings from parents of each sex were caused predominantly by a combination of local genetic factors from the source populations, and competition for resources (light, water, nutrients) influenced by both the location of pots in the glasshouse (pots were moved around regularly, still grouped per site) and the number of seeds sown and germinated in each pot.

Therefore I analysed the local difference in height between offspring of hermaphrodites and females, where a high score indicated that seedlings of hermaphrodite mothers were growing at least as well as outcrossed seedlings from female mothers, whereas low scores meant that seedlings of hermaphrodite parents were locally smaller than seedlings of female parents, so potentially had high self-pollination rates.

The effects of site parameters on Hdiff, the difference in growth performance between seedlings of females and hermaphrodites, estimated as a single value per site, were analysed one predictor at a time. Two site parameters were found to have a significantly positive effect on the local difference in seedling height between parent sexes: landscape-scale connectivity index dH, and relative *F. excorticata* density (Table 5.9, Figure 5.7). The models testing individually the effect of altitude, area, site-scale connectivity index ADRA, and pollinator bird densities, didn't identify any significant influence on local seedling growth performance (Table 5.9).

These results show that in sites with low connectivity, and low *F. excorticata* density, seedlings of the self-compatible hermaphrodites are growing more slowly than the necessarily outcrossed seedlings of female trees. Locally low performances of hermaphrodite's progeny are an indication of low seedling fitness, presumably due to inbreeding depression caused by high rates of self-pollination. On Banks Peninsula, isolation was the main cause of inbreeding depression in *F. excorticata* seedlings, whereas improved connectivity between sites or between trees within sites had a positive effect on seedling growth of hermaphrodite's progeny, likely because of lower self-pollination rates.

Table 5.9: Parameter coefficients from the summary output and analysis of deviance table from the Gaussian GLMs assessing the effect of altitude, area, dH, relative *F. excorticata* density, edge, and average number of bellbird and silvereye detected per 5-min count (data 2005-16) in individual models, on the difference between mean seedling height of hermaphrodite and female *F. excorticata* parent. Bold p-values indicate a significant effect ($p < 0.05$).

Resp. var.	Parameter	Coef.	Std. err.	Df	Deviance	Res. Df	Resid. Dev	p(>F)
Hdiff	Intercept	-30.437	12.01303			7	2320.3	
	Altitude	0.055	0.02693	1	946.7	6	1373.6	0.088
	Intercept	-24.320	15.013			7	2320.3	
	log(Area)	6.282	5.436	1	422.52	6	1897.8	0.292
	Intercept	-8.877	3.940			7	2320.3	
	log(dH)	13.702	3.846	1	1575.6	6	744.72	**0.012**
	Intercept	-6.304	5.107			7	2320.3	
	log(ADRA)	5.876	2.499	1	1112.7	6	1207.7	0.057
	Intercept	-50.005	8.900			7	2320.3	
	FEdensity	18.418	3.711	1	1865.8	6	454.56	**0.002**
	Intercept	-12.250	20.313			7	2320.3	
	Bellbird	6.367	7.151	1	264.59	6	2055.8	0.446
	Silvereye	-5.265	9.573	1	117.26	5	1938.5	0.606

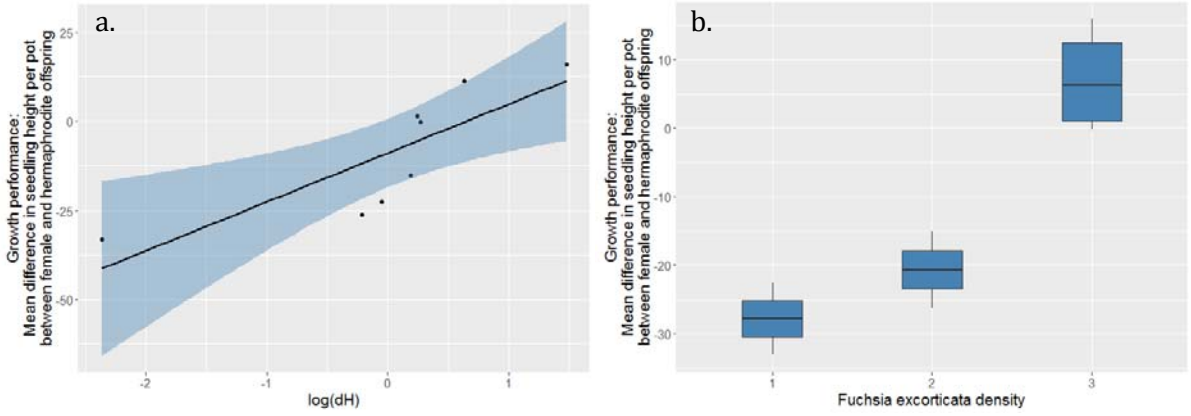

Figure 5.7: Boxplot and scatter plots with fitted regression lines of parameters with a significant effect on the mean difference between mean seedling heights of hermaphrodite and female *F. excorticata* offspring: (a) log(dH), and (b) relative *F. excorticata* density.

Inbreeding depression

The various measurements of inbreeding depression tested in the models were differently affected by fragmentation parameters.

The lack of sufficient outcrossing pollen, resulting in ovule abortion and reducing the mean number of seeds per locule in *F. excorticata* fruits, was affecting females more than hermaphrodites. On female trees, the mean number of seeds per locule increased significantly with area, especially in small sites, with dH, and with bellbird density. Hermaphrodites always had locally higher numbers of seeds per locule than female, however there was a significant variation between site, which was mostly caused by significantly lower amounts of seeds per locule at low-density sites than at other sites, and in forest interior than at forest edge.

There was no difference in germination rate between offspring of females and hermaphrodites, but for both sexes combined the percentage of seeds that had germinated 3 months after sowing tended to be higher in sites with higher densities of bellbird.

Growth performance was generally better for seedlings of female mothers, but the difference in seedling height 5 months after sowing was reduced in sites with high landscape-scale connectivity dH and high *F. excorticata* density. The locally poor performance of seedlings from hermaphrodite mothers seemed to suggest the occurrence of higher self-pollination rates as a result of isolation.

Overall, dH and *F. excorticata* density had a consistent positive effect in reducing inbreeding depression across boss sexes, by increasing female seed production and improving seedling fitness among offspring of hermaphrodites.

IV. Discussion

Inbreeding depression in the early stages of F. excorticata regeneration

In a study assessing the regeneration success of *F. excorticata* from seed production in adults to offspring's establishment and maturing success in the field, Robertson et al. (2011) found that inbreeding depression was low in the earliest stages of reproduction. However, high levels of inbreeding depression were detected in seedlings, with significantly lower survival and growth rates of selfed than outcrossed offspring, to the point that in one site too few selfed seedlings had survived in pots to carry out a transplant experiment, whereas in another site the 7.5-years-old transplanted selfed seedlings were over 70% smaller and had higher mortality rates than outcrossed seedlings (Robertson et al. 2011). The overall inbreeding depression level of 84% estimated in one *F. excorticata* population was probably underestimated, as it didn't compare the fecundity of selfed and outcrossed offspring, yet it was very high in comparison to inbreeding depression rates of other species (Husband & Schemske 1996), and seemed to

indicate the unlikeliness for selfed individuals to reach reproductive maturity (Robertson et al. 2011).

Because of the limited duration of my study, inbreeding depression was only measured at the initial stages of *F. excorticata* regeneration: seed set, germination, and early seedling growth. In Robertson et al.'s experiments (2008, 2011), outcrossed offspring of hermaphrodites and females were performing equally, and the poor performance of selfed offspring was hardly detectable at the seed and germination stages: fruit set on hermaphrodites was only 12% higher than on females, there was no significant difference in seed set between fruits from self- and cross-pollinated flowers, and germination rates of selfed seeds were only between 14% and about 40% lower than germination rates of outcrossed seeds.

In females, inbreeding depression due to the lack of interactions with pollinators is manifested by the production of fewer filled seeds per fruit than in sites where pollination service is sufficient. In my study, the number of filled seeds per locule was significantly lower in female than in hermaphrodite fruits across all sites, reflecting the difference in mean quantity of pollen reception between female and hermaphrodite flowers, due to the ability of hermaphrodites to self-pollinate. Despite this self-compatibility, there was a significant variability between sites in the quantity of filled seeds per locule in hermaphrodite fruits, which may be due to population-specific differences in herkogamy, a flower trait known to influence local self-pollination rates (Robertson et al. 2008).

Inbreeding depression in hermaphrodites is detected through the poor performance of self-pollinated offspring. Locally significant differences in offspring performance in favour of females are an indication of high field rates of self-pollination. At the germination stage, I found no significant difference between parent sexes in the final proportion of seeds germinated 3 months after sowing. This is consistent with Robertson et al. (2011) who found that the detection of inbreeding depression was low for *F. excorticata* at the germination stage. Young seedlings displayed higher inbreeding depression: the necessarily outcrossed progeny of females had grown significantly faster overall than the progeny of hermaphrodites, with locally important differences in seedling heights between parent sexes in favour of female parents suggesting high self-pollination in hermaphrodites.

Inbreeding depression significantly affected by isolation and low population density

Site parameters significantly affecting inbreeding depression at the seed production, germination, and early seedling growth stages included landscape-scale connectivity parameter dH, area, and subjective estimation of *F. excorticata* population density. Given that inbreeding

depression is the consequence of a lack of interaction with pollinator birds, it was expected to be affected by the similar site parameters that had an effect on pollination of females. Indeed, insufficient deposition of outcross pollen leads female flowers to produce a reduced amount of healthy seeds, and hermaphrodite flowers to rely on self-pollination for the production of seeds that appear to be less fit overall for germination and seedling growth than outcrossed offspring (Robertson et al. 2008; 2011).

Connectivity index dH, which is a measure of the importance of each site to the overall landscape connectivity, had a strong and constant effect on inbreeding depression: the number of seeds per locule produced by female trees and the speed of seedling growth among the progeny of hermaphrodites both increased significantly with increasing connectivity. The models also found a significant effect of pollinator birds on the various measures of inbreeding depression, female seed set and germination rates both increasing with bellbird density. This result coincides with the significantly positive effect of dH on local bellbird densities (Chapter 2). For *F. excorticata*, inbreeding depression resulting from reduced pollen flow due to spatial isolation was also detectable within sites: on Banks Peninsula, the seed set of hermaphrodites was significantly lower in sites with low *F. excorticata* population density, and the difference in seedling height between the progeny of hermaphrodites and females was particularly important, with comparatively lower performance of hermaphrodite progeny, in native forest fragments with scarce populations. This difference in growth performance was reduced significantly towards locally higher *F. excorticata* density categories, suggesting the occurrence of higher self-pollination rates at sites with longer distances between flowering trees, likely because of increased within-tree movements by pollinator birds as predicted by Charnov's optimal foraging theory (1976). This is consistent with the significantly higher pollen load scores measured on both female and hermaphrodite flowers at low-density sites (Chapter 3), and seems to agree with the suspicion of higher outcrossing rates at higher *F. excorticata* densities, as observed in various flowering species (e.g. Van Treuren et al. 1993; Mustajarvi et al. 2001).

Other studies assessing the effects of habitat fragmentation on inbreeding depression also found that connectivity rather than area was critical to maintain sustainable gene flow and limit local levels of inbreeding depression. Thus, Lennartsson (2002) showed that habitat fragmentation of the grassland biennial *Gentianella campestris* was responsible for increased self-pollination rates in plants with low herkogamy, and reduced seed set in herkogamous individuals, with high inbreeding depression levels detected among the progeny of both herkogamy types due to low pollinator densities in spatially isolated habitat patches. Reduced connectivity between patches was caused by the un-penetrability of the surrounding matrix, which obstructed pollinators' movements, and had a significantly negative effect on the plant

population viability even in relatively large populations (Lennartsson 2002). For the insect-pollinated, bird-dispersed tree *Sorbus aucuparia*, Bacles et al. (2004) found evidence that the lack of connectivity between fragments at the insect scale was responsible for limited pollen flow among them, causing an increase in local genetic differentiation. However, inter-patch connectivity was maintained at the bird scale, allowing for efficient dispersal to sustain continuous gene flow between remnant fragments and preventing the detection of inbreeding depression locally despite the reduced pollen dispersal (Bacles et al. 2004).

Scattered single trees and small sparse populations of *Gomortega keule*, an endangered Chilean tree, were shown to maintain sufficient inter-patch connectivity for its insect pollinators, which were thus able to provide successful long-distance pollen dispersal service between remnant patches. The resulting wide network of gene flow and overall genetic diversity were sufficient to limit the risk of inbreeding and local extinction within the highly fragmented population (Lander et al. 2010). On Banks Peninsula, the significantly positive effect of dH and negative effect of area on the reduction of local inbreeding depression are indications that the importance of well-connected forest patches of any size containing *F. excorticata* trees is similarly higher than the presence of large populations for the maintenance of sustainable pollen flow and the limitation of local inbreeding depression.

Local consequences of F. excorticata inbreeding depression

Inbreeding depression among isolated *F. excorticata* populations as a result of a local lack of interaction with pollinator birds resulted in reduced production of seeds by female trees and low fitness among hermaphrodite progeny, likely because of locally high self-pollination rates. High inbreeding depression in *F. excorticata* had been detected by (Robertson et al. 2011), who found that adult trees were not highly inbred, as a consequence of the high mortality of selfed offspring. *Sophora microphylla*, another widespread, highly attractive bird-pollinated and self-compatible native tree, was also found to suffer high inbreeding depression because of reduced bird densities (Robertson et al. 2011; Van Etten et al. 2015). This raises major concern for less attractive bird-pollinated native species with lower nectar rewards or less conspicuous flower displays, which may suffer from even lower bird visitation and possibly high self-pollination rates when self-compatible, with the production of fewer or less fit offspring (Van Etten et al. 2015).

For both species, the late detection of inbreeding depression along the plant regeneration process (post-germination) had led to the conclusion that the production of large seed set and numerous seedlings shouldn't be considered an indication of recruitment success,

because of the possibility of these offspring to be selfed with a very low survival probability. In the present study, field evidence of inbreeding depression was not obvious at the germination stage, but was detectable as early as at the seed production phase, with locally significant differences in filled seeds per locule between sexes in favour of self-compatible hermaphrodites. This consequence of locally reduced pollen flow may have detrimental effects on the evolution of sex-ratio in a population, because the production of females relies entirely on the successful regeneration of female trees (which make 50% offspring of each sex, unlike hermaphrodites who produce 100% hermaphrodite offspring, Godley & Berry 1995). Reduced seed set in females may thus lead in the long term to the local loss of gynodioecy (Robertson et al. 2011). Inbreeding depression among seedlings was detectable as early as 5 months after sowing, causing locally high difference in seedling height between the progeny of females and hermaphrodites in favour of the necessarily outcrossed female offspring.

V. Conclusion

Measuring seed production, germination rates and seedling height among the progeny of female and hermaphrodite *F. excorticata* trees in native forest fragments on Banks Peninsula, I detected high inbreeding depression reflecting poor outcross pollen income in isolated sites. Inbreeding depression in *F. excorticata* had been shown by Robertson et al. (2011) to be detectable only at late development stages, with traditional counts of fruit set and seedling quantity being likely to give false results of recruitment success where self-pollination rates are high. Nevertheless, I found that a comparison of field rates of progeny performance between female and hermaphrodite parent trees allowed to detect evidence of locally insufficient pollination service, as a significantly reduced number of seeds produced in female fruits, and as a significantly slower growth of seedlings from hermaphrodite mothers.

Site connectivity appeared to be the most influential fragmentation parameter on local inbreeding depression levels, which is consistent with the significant increase in pollinator bird densities with increasing dH on Banks Peninsula (Chapter 2). Area only had a positive effect on seed quantity of females, the absence of a detectable effect of area on local germination rates and seedling performance contrasts with the common observation that increased patch size generally reduces the detrimental effects of habitat fragmentation on species persistence (Henle et al. 2004; Ewers & Didham 2006), but is consistent with the detection of fewer pollinator birds in the larger sites (Chapter 3). Given the absence of a positive effect of patch area on offspring fitness, it is

important to recognize the contribution of small patches as valuable sources for the maintenance of a sustainable breeding *F. excorticata* population across the fragmented landscape, as previously concluded for other flowering species (Lander et al. 2010). For practical implications on conservation practice, this result is a confirmation that to favour cross-pollination by birds in forest fragments, even small patches are worth protecting. Additionally, population enhancement using local planting of genetically suitable individuals may be carried out where flowering tree densities are too low to prevent high mono-parental pollination as a result of increased within-tree movements of pollinators (Lander et al. 2010).

CHAPTER 6:

Synthesis

Tipperary Gully, the smallest (2.84) and most isolated lowland forest fragment among my study sites on Banks Peninsula, had poor dispersal service (low fruit removal rates) and high inbreeding depression (slow growth of hermaphrodite seedlings) because of its poor connectivity.

(Photo Marine Aubert)

The main objective of this thesis was to assess the effects of forest fragmentation on plant-bird mutualisms in various sized forest patches, and their consequences for the local regeneration of native forest plants relying on birds for reproduction. This chapter synthesises the main research findings, and uses information from complementary studies to put these results in perspective and address some implications for conservation practice in New Zealand.

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I. Effects of forest fragmentation on plant-bird mutualisms

In New Zealand, habitat loss and predation by introduced mammals have caused a drastic decline in the density and diversity of the native avifauna (Holdaway 1989; Holdaway 1999; Innes et al. 2010). This is of particular concern for the important proportion of native plants that rely on birds for pollination and seed dispersal (Kelly et al. 2010), because bird declines have already proven responsible for local mutualism failures and plant population decline due to inbreeding depression (McNutt 1998; Anderson et al. 2006; Robertson et al. 2008; Robertson et al. 2011; Anderson et al. 2011; Wyman 2013). Reduced gene flows between and within populations from a lack of interaction with mutualist birds can lead to significant drops in seed production, and self-compatible plants are at particular risk of producing unfit progeny with low survival rates where self-pollination predominates (Anderson et al. 2016).

The study was conducted on Banks Peninsula, a highly fragmented area scattered with native forest remnants of various size and isolation level, surrounded by farmland. The widespread New Zealand native tree *Fuchsia excorticata* was used as an indicator species, because it is both pollinated and dispersed by a few bird species, including the native bellbird and tui, which have been largely reduced in range and density throughout the country (Godley & Berry 1995). *Fuchsia excorticata* is a gynodiecious species; a lack of outcross pollen causes females to suffer pollen limitation leading to the production of low seed set, and causes self-compatible hermaphrodites to suffer inbreeding depression from high rates of self-pollination (Robertson et al. 2008; Robertson et al. 2011). Long-distance dispersal of seeds is required to favour re-colonization opportunities and maintain sustainable gene flow between populations, as local genetic diversity is necessary to limit bi-parental inbreeding, to preserve population resilience, and ensure long-term population persistence (Aguilar et al. 2008).

In the preceeding chapters, the effects of several fragmentation parameters were tested across a range of native forest patches on local mutualist bird densities (bellbird, silvereye, tui, kereru and blackbird), and on *F. excorticata* reproduction stages: pollen load score (PLS) as a measure of pollination service, fruit removal rate as a measure of dispersal service, and three

measures of inbreeding depression: seed quantity per locule, percentage of germination 3 months after sowing, and difference in seedling height between the progeny of hermaphrodite and female parents 5 months after sowing. Fragmentation parameters included area, landscape-scale connectivity index dH, and site-scale connectivity index ADRA. Altitude was included in the analyses because of its influence on New Zealand birds' distribution (e.g. Elliott et al. 2010). Two parameters indirectly related to forest fragmentation were included as categorical factors estimated subjectively: edge effect, and *F. excorticata* population density. Local bird densities were estimated as the average number of birds detected per 5-min count in each site, from various count stations between 2005 and 2016. A summary of the significant effects of each parameter tested in the previous chapters is presented in Table 6.1.

Table 6.1: Effects of various site parameters retained by model selection in generalized linear mixed models, on the number of birds detected per 5-min count in 18 lowland forest fragments on Banks Peninsula (data 2005-2016), and on *F. excorticata* reproduction measures: pollen load score in 13 of these sites, fruit removal in 10 sites, and seeds per locule, germination rate, and difference in seedling height between parent sexes in 11 sites. white: not retained by model selection, green +: positive effect, red -: negative effect, +/-: nonlinear effect (increase then decrease), *: singnificant effect in single-predictor analysis, grey: not tested or not applicable.

Parameter / Tree sex	Mutualist birds	PLS		Fruit removal	Seeds per locule		Germ. rate	Height difference
		F	H		F	H		
Altitude				+				
Area	-	+/-			+/-			
Connectivity (dH or ADRA)	+	+		+*	+			+
Edge						+		
FEdensity		-	-	+		+		+
Mutualist birds					+		+	

Altitude

Altitude ranged from 35 m to 740 m above sea level across all study sites, and didn't have a significant effect on the guild of mutualist birds on Banks Peninsula (Table 6.1). At the species level, the only mutualist bird that appeared to be significantly affected by altitude was

the kereru, which was detected in higher abundance at lower sites (Chapter 2). As observed in other studies (e.g. Elliott et al. 2010), several non-mutualist bird species were also affected by altitude, with native insectivorous forest birds such as tomtit, brown creeper and rifleman significantly increasing, and introduced generalists such as the song thrush significantly decreasing in density along the altitudinal gradient (Chapter 2).

The absence of correlation between mutualist bird densities and altitude may explain the absence of effect of altitude on pollination service and inbreeding depression (Table 6.1). One exception was found in this study, but it seemed to be explained by a bias in the sampling method. Thus in Chapter 4, altitude had a significantly positive effect on fruit removal rate, measured as the proportion of green fruits remaining on a branch and indicative of dispersal service by birds in the middle of fruiting season. The annual start and period length of *F. excorticata*'s reproductive season varies across time between sites, as a result of local differences in temperature and micro-climate, which are naturally related to altitude (Bartholomew 2008). As fieldwork to measure fruit removal rates was carried out in 10 study sites over a short period of time, it is possible that the most elevated sites at that time had naturally few ripe fruits, not because of high dispersal rates, but rather because the ripening season had only just started there at the time of the survey.

Area

The 18 study sites used in this study were lowland native forest fragments ranging from 2.84 ha to 93.44 ha. Among the large and ever-increasing literature on forest fragmentation, there is general consensus on the predominately positive effect of patch area on native biodiversity and ecological interactions (e.g. Stouffer & Bierregaard 1995; Sekercioglu et al. 2002; Wilcock & Neiland 2002; Cordeiro & Howe 2003; Sodhi et al. 2004). There is global evidence that following habitat loss and forest fragmentation, many types of native forest birds, including insectivorous species, flocking birds, small ground-nesting birds, large tropical birds, and canopy frugivores, occur in significantly lower densities in small forest patches (usually taken to mean smaller than 10 ha) than in larger forest fragments (Stouffer & Bierregaard 1995; Sekercioglu et al. 2002; Sodhi et al. 2004). Surprisingly, in this study the effect of area on mutualist birds and their interactions with *F. excorticata* was nearly always non-significant, or negative among the larger sites (Table 6.1).

Although area had no significant effect on local abundance of individual bird species, apart from a mild increase in fantail density toward larger sites (Chapter 2), the guild of pollinator and disperser birds was detected in significantly higher abundance in small sites

(Table 6.1). Interestingly, a recent study also carried out on Banks Peninsula had found no significant effect of patch area on bird density and diversity (Barbaro et al. 2012). Highly mobile honeyeaters such as the bellbird are known to feed commonly at forest edges and in forest gaps as well as in forest interiors, and have been regularly reported fly between forest patches across farmland (Spurr et al. 2010), therefore they may not be as severely impacted by the reduction in size of forest fragments as other, more sensitive birds (Sodhi et al. 2004). Yet, the reason for a negative effect of area on mutualist bird densities remains unclear.

Possibly as a result of the decrease in mutualist birds with increasing area, dispersal service, germination and growth rates were not affected by patch area (Table 6.1). The beneficial effect of increased area observed elsewhere for pollen and seed dispersal (Wilcock & Neiland 2002; Cordeiro & Howe 2003; Harris & Johnson 2004) was detectable on Banks Peninsula only on pollination service of females in sites smaller than 15 ha, and similarly on female seed set also in small sites, but that tendency was then reversed with a significant decrease in pollen load scores and number of filled seeds per locule recorded in large sites (Chapters 3-5). Thus, plotted data graphically displaying the numerical relationship between area and the various measures of plant-bird interactions generally showed mild slopes, often driven by poor values from the two largest forest fragments, Mount Sinclair and Hinewai (respectively 75 ha and 93 ha of native forest within the much larger total area of the reserves). A previous study on *F. excorticata* reproduction across New Zealand had also measured particularly low pollen scores on female flowers in Hinewai (Robertson et al. 2008), so the apparent lack of local pollination service seems to be constant there. In these two particular sites (Mt Sinclair and Hinewai), native pollinator birds were found in Chapter 2 to occur at densities as high as in pest-free bird sanctuaries (Murphy & Kelly 2001), therefore the apparent mutualism failure cannot be attributed to low densities of mutualist birds. Instead they are presumably due to low visitation rate by birds to *F. excorticata* flowers, as reported by Robertson et al. (2008).

The possibility that this measured failure in mutualistic interactions may result from local measurement bias should be considered. In both sites, the majority of the inflorescences available to birds on *F. excorticata* trees were located high in the canopy, with limited flowers and fruits reachable by hand from the ground to a human observer, unlike in the other sites. If nectar and fruit feeding by birds was mostly occurring around tree tops in the two larger sites, a behaviour previously observed for bellbird in other New Zealand forest fragments (Bell 2010), local sampling on the canopy would provide results of better accuracy. However, working with bellbird pollination on a different pollen-limited plant species (*Peraxilla tetrapetala*) in inland Canterbury, Robertson et al. (2008) found no effect of flower height in the canopy (between 1

and 15 m above ground) on bellbird pollination rates, which suggests that this may not explain the lower *F. excorticata* pollination in Mt Sinclair and Hinewai.

Connectivity

Patch connectivity among fragmented habitats has been measured in ecological studies using a wide range of metrics, none of which appearing to be obviously the most suitable for the purpose of my research (e.g. Jordán et al. 2003; Pascual-Hortal & Saura 2006; Saura & Pascual-Hortal 2007; Bodin & Saura 2010; Baranyi et al. 2011; Ernst 2014). After comparing six different measures of site connectivity in Chapter 2, I settled on two indices: landscape-scale dH, which represents the importance of the contribution of each individual patch to the overall landscape connectivity or Harary index H, and site-scale connectivity ADRA or Area to Distance Ratio, which only takes into account the neighbouring patches to each individual fragment. Both were calculated using an estimated connectedness distance of 500 m, based on estimations of bellbird's regular travel distances between forest patches across open land (longer distances have been reported but at lower frequencies, Spurr et al. 2010). The two indices were not highly correlated (Chapter 2), therefore they were not expected to have similar effects on bird populations, mutualist interactions and inbreeding depression.

Local density of pollinators and disperser birds was positively affected by dH (Table 6.1), which also had a positive effect specifically on bellbirds and silvereyes, whereas ADRA had no significant influence on the guild of mutualists but was associated with increasing numbers of native forest birds such as kereru, tomtits and riflemen (Chapter 2). It is thus unsurprising that dH was the fragmentation parameter influencing local mutualisms with birds and regeneration success of *F. excorticata*, unlike ADRA which only had a positive effect on pollination service (Table 6.1). Fruit removal rates, seed quantity per locule in female fruits, and difference in seedling heights between hermaphrodite and female progeny, all significantly increased with dH (Chapters 4-5). In Chapter 3, no significant effect of dH was detected on pollen load scores of female flowers, however its positive effect on inbreeding depression confirmed the local increase in pollination service with dH (Chapter 5), which may have been masked in Chapter 3 by a confounding negative effect of area in large sites. Indeed, high numbers of female seeds per locule are representative of the locally high quantity of pollen received by the female flowers, while an increase in seedling height difference (from negative to around zero) between parent sexes suggests a reduction in self-pollination.

The significantly positive effect of patch connectivity to plant-bird mutualisms observed on Banks Peninsula is consistent with similar findings in other studies (e.g. Lennartsson 2002;

Cordeiro & Howe 2003; Cramer et al. 2007; Herrera & Garcia 2010). For *F. excorticata*, a tree both pollinated and dispersed by a few bird species with relatively high mobility, the levels of connectivity required to achieve sufficient pollination and dispersal service are equivalent. For plants relying on different organisms for pollination and seed dispersal, the local connectivity level may be suitable to one mutualism but not to the other, the mutualism disruption thus possibly leading to adverse genetic consequences on the genetically isolated population (Bacles et al. 2004).

Vegetation structure: F. excorticata density and edge effect

While geographical attributes of forest fragments such as altitude, patch area and connectivity have been shown to have a direct effect on local bird density, and as result on plant-bird mutualistic interactions, some site characteristics may affect mutualism success because of their influence on competition and foraging behaviour, including local bird abundance and species diversity (Pyke et al. 1977; Craig et al. 1981; Fontaine et al. 2008).

A naturally competitive behaviour of the tui, commonly observed where co-occuring with other honeyeater species such as bellbird and stitchbird, was shown to favour shorter feeding times per flowering plant by smaller nectarivores and to increase the odds of successful cross-pollination (Anderson 2003). The low abundance of the recently reintroduced tui on Banks Peninsula (estimated at around 100-150 birds in 2016, Laura Molles pers. com.), is preventing the occurrence of this common competitive behaviour against the smaller bellbirds and silvereyes, with unknown effects on their foraging behaviour.

The species composition of bird assemblages in New Zealand native forests is characterized by higher numbers of native birds in forest interiors and higher numbers of exotic birds at forest edges (Barbaro et al. 2012), a difference that isn't necessarily detectable by standard 5-min counts in small fragments. However, no significant edge effect was identified on pollination, seed dispersal or inbreeding depression (Table 6.1). In Chapter 5, model selection revealed a significant increase in seed quantity of hermaphrodite fruits from forest interior, through forest tracks, to fragment edge, suggesting a slight preference of pollinator birds to feed on *F. excorticata* nectar in forest interiors than in open environments. Although similar negative edge effects on plant-bird mutualisms have been commonly reported worldwide among bird-pollinated plants, this is not always the case; there has even been evidence in New Zealand that bellbird was providing better pollination service to the declining mistletoe *Peraxilla tetrapetala* at forest edges (Burgess et al. 2006). These edge effects on bellbird foraging strategies may not be contradictory: the attractiveness of flowering plants to pollinators is often related to the

conspicuousness of flower display and accessibility of inflorescences (Burgess et al. 2006), both being achieved at forest edges for *P. tetrapetala* (Burgess et al. 2006), and possibly in the forest canopy for *F. excorticata* (Bell 2010).

The local density of a plant population may also affect its overall conspicuousness and attractiveness to mutualist birds moving across a fragmented landscape, therefore potentially affecting interactions with birds. Charnov's optimal foraging theory (1976), predicts that in low-density plant populations, mutualists will feed more thoroughly within single plants and move between individual plants less often than in high-density populations. As a result, outcrossing rates would be expected to be higher at high plant densities, while self-pollination rates may be higher at low densities, irrespective of population area. This theoretical pattern has proven consistent with observations made on various plant species and their pollinators or seed-dispersers (e.g. Van Treuren et al. 1993; Mustajarvi et al. 2001; Weber & Kolb 2013).

In the present study, *F. excorticata* density had not been measured as a continuous variable using quantitative methodology, so the study sites were classified subjectively into low-, medium-, and high-density populations based on personal field observation at the sampling areas. For this reason, no linear effect can be extrapolated from the results, which should be interpreted as apparent trends worth exploring in future experiments. On Banks Peninsula, the effect of *F. excorticata* density was negative on the pollen load scores of females and hermaphrodites, and positive on fruit removal rate, on hermaphrodite seed quantity per locule, and on the difference in height between hermaphrodite and female seedlings (hermaphrodite seedling performance increasing from negative to null in comparison to female seedlings, reaching similar growth rates between female and hermaphrodite progeny at high density sites). Significantly higher pollen load scores at low-density sites indicates that, limited by resource availability, optimal pollinators' foraging strategy led to more thorough visitations of individual plants than in forest patches where *F. excorticata* nectar wasn't a limited resource. As the pollen scores on hermaphrodites were higher at low plant density, higher self-pollination rates would be expected there because of the contribution of birds to geitonogamous breeding in addition to the natural rates of self-pollination. The lower seed quantities in hermaphrodite fruits at low-density sites, and the locally bad performance of hermaphrodite progeny showed by the important difference in seedling height compared to female progeny (Height(hermaphrodite) – Height(female) < 0), seemed to confirm the occurrence of locally high self-pollination rates.

II. Implications for conservation practice in New Zealand

Using the example of *F. excorticata*, this study set out to improve the ecological knowledge on plant-bird interactions and native plant regeneration in the New Zealand context of high forest fragmentation and native bird decline. Based on these results and other relevant studies, several recommendations can be made for the purpose of assessing individual habitat patches for local indicators of plant-bird mutualisms and plant regeneration success, and for maintaining or restoring sustainable pollination and dispersal service by birds.

Using F. excorticata as an indicator to assess plant-bird interactions in fragmented forests

As *F. excorticata* nectar is a preferred food for the native honeyeaters, local pollination failure in *F. excorticata,* or in similarly widespread, high-reward native flowering plants, is likely to indicate a disruption in pollination of other bird-pollinated plants (Van Etten et al. 2015). Bird-pollinated plants with low nectar reward, restricted plant distribution, or inconspicuous flower displays are at particular risk of being disregarded by locally reduced populations of pollinator birds (Van Etten et al. 2015). As a result, self-compatible species constrained to high rates of self-pollination may suffer inbreeding depression with the seemingly successful production of abundant progeny but cryptically disabled by low fitness and high mortality (Robertson et al. 2011; Van Etten et al. 2015). However, when continuous gene flow is maintained through efficient seed dispersal, the detrimental consequences of poor pollination including inbreeding depression may be reduced (Bacles et al. 2004).

Theoretically, dispersal failure may be responsible for the disruption in gene flow between populations, ultimately reducing local genetic diversity and causing genetic bottlenecks in isolated populations (Sork & Smouse 2006). However, studies measuring the field consequences of dispersal failure for New Zealand native plants are lacking (Kelly et al. 2004; Robertson et al. 2006). Local extinction risk due to dispersal failure alone depends on various factors described by Bond (1994) and termed "mutualist service", "mutualist-dependence", and "seed-dependence." in Kelly et al. (2004). The guild of *F. excorticata* dispersers is generally diverse and abundant on Banks Peninsula, *F. excorticata* seeds do not depend on the passage through a bird's gut to germinate, and *F. excorticata* is a widespread, long-lived species that does not require high rates of regeneration for population persistence (Burrows 1995; Godley & Berry 1995; Robertson et al. 2008), therefore dispersal failure alone is unlikely to cause local extinction. This echoes the conclusion of recent studies, which considered that for the New Zealand flora in

general, dispersal failure may generally be worrying only when occurring conjointly with pollination failure (Kelly et al. 2004; Kelly et al. 2010; Anderson et al. 2016).

In this study, I found that the local disruption in plant-bird mutualisms was driven mostly by poor connectivity, both between populations (low site connectivity within the fragmented landscape) and perhaps also between individual trees within populations (low visually assessed plant population density). The consequences of spatial isolation on *F. excorticata* populations included reduced densities of mutualist birds as well as non-mutualist native forest birds, low pollination rates of females resulting in reduced seed quantity in female fruits, high rates of self-pollination causing poor growth rate of hermaphrodite progeny in comparison to the necessarily outcrossed female progeny, and low fruit removal rates indicating dispersal failure. To decrease the local extinction risk triggered by combined pollination and dispersal failures in isolated sites, the restoration of local connectivity may be necessary.

Restoring local connectivity

The main findings of this study are the overall importance of patch connectivity, and the relative unimportance of patch area, for sufficient interactions with birds to ensure both pollination and dispersal success (small patches < 5 ha with relatively high dH did not suffer mutualism failure), and by extension to ensure local long-term persistence of native plants relying on birds for their reproduction. An implication in terms of conservation is that theoretically even small forest fragments should be suitable for protection, provided that sufficient connectivity is maintained and local causes of biodiversity loss are controlled in order to avoid further decline in local biodiversity (Lander et al. 2010).

The calculation of site connectivity depends on the target plant species and its mutualist partners: in the case of *F. excorticata* used in this study, an average connectedness of 500 m between forest fragments was estimated based on reports of bellbird travel distance, keeping in mind that bellbird are able to achieve much longer travels on less frequent occasions (Spurr et al. 2010). This distance may be adjusted to match the mobility of other mutualist species, i.e. probably shorter for insect pollinators, or longer for the dispersers of large-seeded trees. Processing GIS data with the software Conefor (Saura & Torne 2012) will allow for the calculation of the Harary index: the overall landscape connectivity of the region in which the fragment of interest is embedded, and the importance dH of each fragment to the current landscape connectivity. A high value in comparison to that of other patches in the landscape will indicate that the fragment may be a key node in the network of ecological processes in which the mutualist

partners are involved. A low dH can be an indication that some mutualistic interactions may be locally disrupted.

When a site is identified as ecologically isolated from other sources of pollen and seeds, the local loss of genetic diversity may be reversed by increasing its connectivity within the landscape. If plantation efforts are considered, expanding the size of an existing isolated site is not expected to improve the long-term persistence expectancy of a plant population. Alternatively equivalent efforts may be successfully used in establishing small stands of flowering trees in the surrounding matrix, strategically located between the isolated fragment and other patches containing populations of the same species. The addition of such ecological nodes in the overall network of species interactions would be beneficial not only to increase the reproductive connectivity of isolated fragments, but also to increase the overall connectivity of the whole system of patches in the landscape (Bodin & Saura 2010; Baranyi et al. 2011). Small patches and even single standing trees have been shown to participate in the maintenance of sufficient gene flow between forest fragments, locally increasing both outcrossing rates and seed dispersal rates (Herrera & Garcia 2010; Lander et al. 2010). Indeed, scattered trees could be used by nectarivores as nectar sources, thus as pollen sources participating in pollination processes between populations, and by frugivorous birds as potential food sources but also as perches favouring the deposition of seeds of various species, thus increasing gene flow between populations of several plant species (Herrera & Garcia 2010; Lander et al. 2010).

Additional enrichment sowing or planting may be considered in sites where a low plant population density is responsible for an overall low genetic pool contributing to the next generation, and to locally high rates of geitonogamous inbreeding due to birds distributing pollen among the flowers of a single tree, and where field rates of seed migration are too low to maintain sustainable genetic diversity (Lander et al. 2010). However, the regeneration of bird-deposited seeds may be prevented by local environmental factors, such as seed predation, in which case conservation strategies may aim at enhancing micro-habitat suitability through seed predator control for example before undertaking plantation programs (Herrera & Garcia 2010). For local population enrichment as well as for the restoration of patch connectivity, the seeds or seedlings used in plantation projects should be carefully sampled following standard procedures in order to suit local genetic diversity both at the patch and regional scale (Broadhurst et al. 2008).

Since the values of biodiversity conservation have reached general awareness, there have been growing efforts to try and protect a maximum of the remaining native biodiversity, with the aim of mitigating or sometimes reversing some of the loss of species and habitat caused by the conversion of native forest into farmland. Thus, the usefulness of protecting small, potentially unsustainable fragments has often been questioned. Based on the results of this research, in

highly fragmented yet relatively well connected landscapes such as Banks Peninsula, small forest fragments of just a few hectares appear capable of hosting sufficient mutualistic interactions to ensure the regeneration of native plants relying on birds for their reproduction. Therefore, provided that this connectivity is maintained, the protection of a small forest fragment is not only worthwhile for the conservation of its local biodiversity, but also for the enhancement of various ecological processes occurring throughout its surrounding landscape.

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